

TEXTBOOK OF NEURO-ANATOMY
AND
THE SENSE ORGANS

TEXTBOOK OF NEURO-ANATOMY AND THE SENSE ORGANS

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PREFACE

This book has been written primarily for the first year medical student who is receiving instruction in the intricate anatomy of the nervous system. It is hoped it will also serve others with approximately equivalent previous training who have an interest in the subject. The material has been gathered from monographs, textbooks of anatomy and physiology and from the journals. The arrangement and organization of the material is based upon the author's experience as a teacher of first-year medical students.

The sense organs are given somewhat more attention than is necessary from a strictly neurological standpoint. This has been done because in many laboratories the sense organs are studied in connection with the nervous system rather than with the course in Histology and Microscopic Anatomy. The general treatment has been by functional systems, and considerable emphasis has been placed on functional aspects of the various divisions of the nervous system. Also considerable use has been made of comparative anatomy because of the aid to understanding of structure and function which this affords. The entire purpose has been to give the student a conception of the nervous system as a living active mechanism.

The figures of the spinal cord and part of the brain stem have been drawn in outline from Pal-Weigert sections and schematized on the right hand side to show positions of cell groups, fiber tracts, etc., as indicated in various monographs and other literature of neuro-anatomy. The left hand side has been filled in to show the appearance of the fibers in the sections from which the drawings were made. It is hoped that this arrangement will enable the student to interpret more readily in functional terms the sections of brain stem and spinal cord usually provided for study.

As an introduction to interpretation of clinical neurological pictures by the student a brief description of some lesions in various parts of the nervous system has been inserted at the ends of a number of the chapters. To avoid confusion and to keep the anatomical basis of interpretation in the foreground these lesions and their effects have been stated simply and concisely. The purpose of the entire presentation is to aid the student to think as early as possible in terms of functional anatomy.

In preparing a book of this type one becomes indebted to so many individuals for suggestions and aid that it is impossible to make acknowledgment to all. I wish, however, to express my special indebtedness to Dr. Andrew T. Rasmussen and to Dr. D. W. E. Baird. To Dr. Ralph A. Fenton, who has read part of the manuscript, and to my colleague, Dr. William F. Allen, who has critically read all of it, my thanks are also due for criticism and help.

Portland, Oregon.

OLOF LARSELL.

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CHAPTER 1

TROPISMS AND SIMPLE NERVOUS MECHANISMS

Protoplasm, "the physical basis of life," has certain fundamental properties which distinguish it from nonliving substance. Among the chief of these are irritability and the power to conduct stimuli. In the Protozoa, composed of a single cell, irritability, or the power to receive stimuli, together with the ability to transmit the impulses produced to points removed from the field stimulated, are both properties of the individual cell. In addition the cell also performs the functions of metabolism, reproduction and other vital processes. It is usually stated that conduction is protoplasmic, the impulse traveling through the cytoplasm of the cell from the point stimulated. It has been shown that in some Protozoa, at least, there is a specialization of parts of the cell into an elaborate neuromotor system. This consists, e.g., in *Paramecium* (Rees, 1921), of a neuromotor center, located anteriorly in the cell, from which radiate peripherally directed fibrils. These fibrils are connected with the basal granules of the cilia and with the trichocysts. These systems conduct impulses and coördinate the movement of cilia. There is thus found, even in one-celled animals, a specialized mechanism whose function is to bring about relatively quick responses of purposeful value to the organism.

The various types of stimuli which produce response have been studied and classified under the general name *tropisms*. If an amoeba is touched with a glass rod, for example, or other mechanical stimulus be applied, it will respond by a flow of its protoplasm away from the point stimulated. The flow of protoplasm begins at a point distant from the stimulus by the formation of a pseudopodium which slowly moves away from the point irritated. Presently the entire mass of protoplasm moves in the same general direction. The fact that the pseudopodium begins the movement before any activity of the main body of protoplasm is noticeable indicates conduction of an impulse through the protoplasm.

Such a movement away from the source of stimulation is called a *negative tropism*. In the case cited it is designated *negative thigmotropism* or response to touch. Other tropisms produce responses toward the source of the stimulus, as for example food. The stimulus afforded by food, which produces a positive response, is designated as positive *sitotropism*. Other tropisms, which may be positive or negative, are *phototropism*, or response to light; *galvanotropism*, or response to an electric current; *geotropism*, or response to the gravitation of the earth; *chemotropism*, or response to stimulation by chemicals, etc. A tropism may be defined as the tendency of protoplasm, whether composing a single cell

the cell processes, as well as by the distribution of certain processes to muscle cells and of others to sensory terminations. The natural path would thus be from the sensory ending or receptor, e.g., a surface of the body, along the stretched fiber (*afferent*) between it and the nerve cell, thence along a second stretched fiber (*efferent*) to the muscle fiber or *effector organ*. As nerve cells became farther and farther separated, in the evolutionary process, by increase of body size of animals and complexity of structure of organs, the cells lost contact with one another. Connections in this type of nervous system are made temporarily by means of the *synapse*, formed of delicate terminal processes of nerve fibers. Thus the nerve network disappeared and a synaptic nervous system was established, according to Parker (1919). Rapid diffusibility of a nerve impulse to all parts of the body was lost but more precise conduction was established. The synapse serves as a one-way gateway for impulses, and is regarded as the governing factor of the marked polarity of conduction in nerve cells. At the synapse there is resistance to the

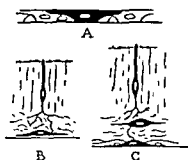


FIG. 1.—EFFECTORS AND RECEPTORS.

A, independent effector. B, simple receptor-effector. C, complex type of receptor-effector systems (After Parker)

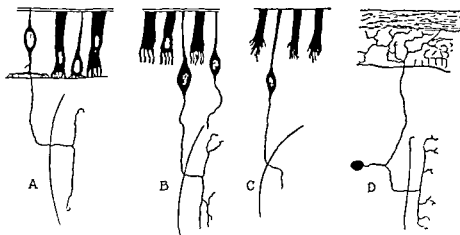


FIG. 2—PHYLOGENETIC DEVELOPMENT OF SENSORY NERVE CELLS AS ILLUSTRATED BY THEIR STRUCTURE IN SEVERAL ANIMAL TYPES. (After Retzius.)

A, neuro-epithelial cell with nerve process to central nervous system as shown in the earth-worm (*Lumbricus*). B, bipolar nerve cell, with peripheral termination in epithelium and central process to central nervous system, as shown in the polychaet worm (*Nereis*). C, sensory nerve cell with cell body migrated farther toward the central nervous system, as shown in a mollusc (*Limax*). D, sensory nerve cell as shown in a vertebrate.

passage of the nerve impulse even in the normal direction and in normal nerve fibers. The impulse is delayed in its normal direction and is entirely blocked in the reverse direction. Certain drugs, such as strychnine, increase the ease with

or a many-celled organism, to react in a definite manner when subjected to external stimulation.

In Metazoa the mechanism of response is much more elaborate, increasing in complexity from the lower to the higher animals and reaching its culmination in the human nervous system.

In the sponges a primitive type of muscle or *effector* tissue is found, but it has no nervous tissue connected with it. Sponges can contract and also can show a slow transmission of certain types of stimuli. This transmission however is regarded as protoplasmic, rather than nervous, conduction. Among the Metazoa, the sponges therefore show one fundamental feature of the *neuromuscular mechanism*, namely, the muscle fiber (Parker, 1919). Associated with this is the property of protoplasmic conductivity which is relatively sluggish, as compared with nervous conductivity.

In Coelenterates there is found a specialization of cells of ectodermal origin into a *nerve net*. This is made up of cells and fibers, connecting adjacent cells, together constituting *protoneurons*, "the primitive cell units of the nerve net" (Parker, 1919). In these the protoplasm is modified so as to have a relatively high rate of conductivity. They are found under the surface epithelium of the body and receive nerve fibers from receptors in the surface ectoderm. They also give off nerve fibers to muscle cells of the body. Through this type of mechanism impulses are rapidly transmitted from any point stimulated to all parts of the body. There is both physiological and structural continuity of the cells of the nerve net, but these cells do not have close relationship with the muscle cells they activate. Conduction is diffuse throughout the net, and the factor which brings about a certain amount of coördinated movement of muscles is that stimuli acting on nerve cells already in activity do not produce new reactions through these cells, i.e., there is a refractory phase of the cells (Rogers, 1927). It has also been suggested (von Uexkuill, 1909) that impulses flow more freely into regions where the nerve net is stretched than into those not stretched. The processes of the protoneurons in stretched areas would thus simulate, temporarily, nerve fibers as found in higher forms.

The nerve net is of interest to the student of the nervous system, both because it represents the most primitive type of nervous system, as shown in Coelenterates and other lower forms, and also because it is regarded by many neurologists as being present in vertebrates, including man, in the intestine and possibly in blood vessels.

The Synaptic Nervous System.—Mention has been made of the apparently greater conductivity of the stretched portion of the nerve net than of the unstretched portions, in Coelenterates. This difference is regarded by many students of the nervous system as the first suggestion of *polarity*, a striking feature of nerve cells of the synaptic type of nervous system. By polarity of nerve cells is meant the property they possess of conducting impulses always in the same direction. Polarity is undoubtedly increased by the lengthening of

TROPISMS AND SIMPLE NERVOUS MECHANISMS

the cell processes, as well as by the distribution of certain processes to muscle cells and of others to sensory terminations. The natural path would thus be from the sensory ending or receptor, e.g., a surface of the body, along the stretched fiber (*afferent*) between it and the nerve cell, thence along a second stretched fiber (*efferent*) to the muscle fiber or *effector organ*. As nerve cells became farther and farther separated, in the evolutionary process, by increase of body size of animals and complexity of structure of organs, the cells lost contact with one another. Connections in this type of nervous system are made temporarily by means of the *synapse*, formed of delicate terminal processes of nerve fibers. Thus the nerve network disappeared and a synaptic nervous system was established, according to Parker (1919). Rapid diffusibility of a nerve impulse to all parts of the body was lost but more precise conduction was established. The synapse serves as a one-way gateway for impulses, and is regarded as the governing factor of the marked polarity of conduction in nerve cells. At the synapse there is resistance to the

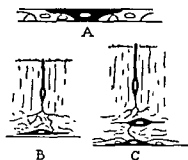


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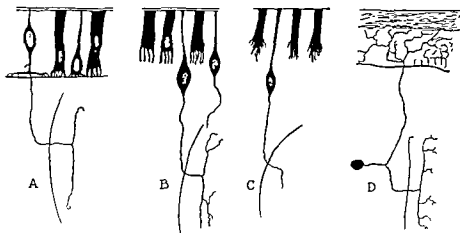


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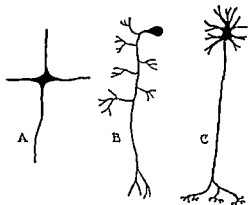


FIG 3—STAGES IN DIFFERENTIATION OF MOTOR CELL TYPES. (After Parker.)

A, protoneuron from nerve net of a coelenterate. B, motor neuron of an earthworm. C, motor neuron of a vertebrate.

very striking and violent. These results indicate the chief stages in the evolution of the synapse.

One result of the separation of the nerve net into anatomically and functionally distinct elements has been development of a number of structural types of nerve cells and fibers. These may be grouped, functionally, into three fundamental categories, namely, *receptors*, *correlators* and *effectors* (Figs. 1-4). The receptors are connected directly or through various modifications in the form of sense organs, to surfaces of the body or to deep end-organs, and receive stimuli of various types. The correlators receive the impulses from the centrally directed branches of the receptors and bring about a correlation with stimuli from other receptors. They are grouped together in large numbers in masses which constitute most of the central nervous system. The effectors convey the result of correlation to motor organs, muscles or glands producing contraction or secretion, as the fundamental responses. These responses are designed to enable the organism to cope with its

which the nervous system of many animals may be stimulated, apparently by lowering the resistance at the synapse. By the use of strychnine it has been shown, by A. R. Moore, that the neuromuscular responses of Coelenterates are not affected, no synapses being present. In Echinoderms, which have a combination of synaptic nervous system and nerve net, some effect is produced. In Crustacea and Molluscs, which have synaptic nervous systems, there is a very marked effect in increasing the response to stimulation. In mammals, as has long been well known, the neuromuscular responses, after strychnine dosage, are

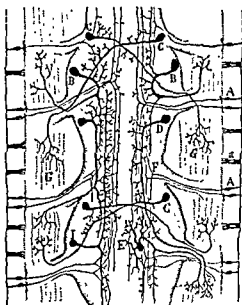


FIG. 4—DIAGRAM OF SENSORY AND MOTOR SYSTEM OF A WORM. (From Cajal, after Retzius and Lenhossek)

A, sensory cell of the cuticle; B, homolateral motor cells of the central ganglia; C, crossed motor cells; D, homolateral longitudinal motor cells; E, multipolar motor cells; G, terminal ramifications of motor neurons on muscle fibers; I, interganglionic association cells.

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environment, to secure food or to carry out the metabolic and reproductive processes.

Anatomically and functionally distinct nervous units of this type having no direct continuity of protoplasm to adjacent nerve cells, are called *neurons*. They constitute the units of which the synaptic nervous system of animals above the Coelenterates is composed. By their arrangement and their polarity they determine the pathways of nervous impulses and the connections of these pathways within the correlation centers of the nervous system. The individual neuron, however, does not function alone but is arranged in chains to form physiological units. These may in turn be connected with other similar units, forming complex pathways. The simplest functional chain consists fundamentally of two neurons. The first receives stimuli from a receptor organ in the skin, in internal epithelial surfaces, or elsewhere. This function is accomplished in the least specialized types by a modification of the cell body or of the peripheral process of the neuron into a receptor mechanism or sensory end-organ. The nerve fiber between the receptor and the correlation center constitutes the afferent conductor. In the correlation center, in which is located the synapse, the impulse is transmitted to the second neuron. The second neuron relays the impulse, through its efferent process, to the effector organ. Here it usually is transmitted through a special modification of the nerve fiber into the muscle or gland which produces the response. This chain constitutes the simplest type of *reflex arc*. It is probable that most reflex arcs, at least in higher vertebrates, consist of more than two neurons, one or more units usually being intercalated between the afferent and the efferent neurons of the arc.

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CHAPTER 2

DEVELOPMENT OF THE NERVOUS SYSTEM

The nervous system is derived in the embryo from a thickened zone of ectoderm, in the mid-dorsal region, called the *neural plate* (Fig. 5, A). The lateral edges of this plate grow at a faster rate than does the middle part, resulting in a *neural groove* (Fig. 5, A'), with a *neural ridge* on each side. By deepening of the groove and by approach toward the mid-dorsal line of the neural ridge from each side (Fig. 5, B and C') with final meeting and fusion, a *neural tube* is formed (Fig. 5, D and D'). The ectoderm of the body surface, with which the neural ridges were continuous up to the time of fusion with each other, separates from the tube of ectoderm and closes above it. The neural tube thus becomes detached and assumes a position below the body surface. Mesoderm migrates between it and the skin ectoderm.

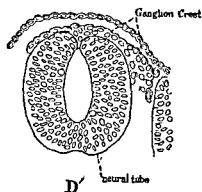
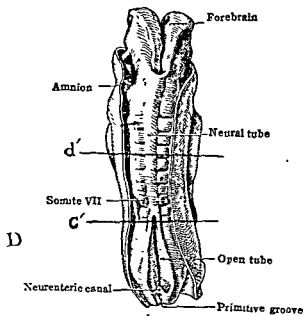
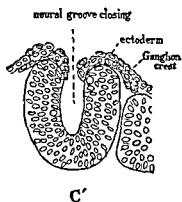
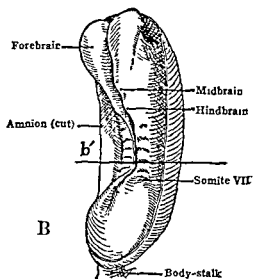
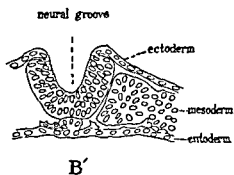
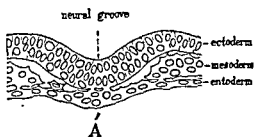
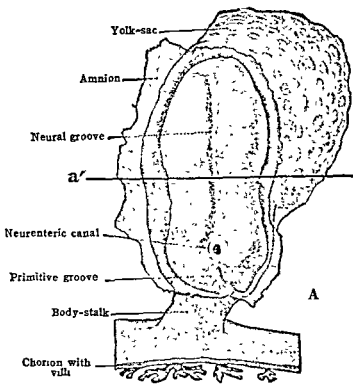
The neural groove begins to close near the middle of the body. The process of closing continues both rostrally and caudally. For a time there is an opening at each end called respectively the *anterior* and the *posterior neuropore*. The formation of the neural tube in the body region results in the spinal cord. By the 15 somite stage of the embryo the closure of the tube has extended forward as far as the forebrain. The anterior neuropore has closed by the 20 somite stage. The posterior neuropore disappears at the 30 somite stage.

Before the brain region closes two constrictions appear, dividing this part of the neural plate into forebrain, midbrain and hindbrain. After closure is completed these regions constitute the primary brain vesicles.

A neural cavity results from the formation of the neural tube. In the spinal cord region this eventually becomes the central canal. In the brain region it is transformed into the ventricles. The neural cavity has an elongated diamond

FIG. 5.—DORSAL VIEW OF HUMAN EMBRYOS AND DIAGRAM OF TRANSVERSE SECTIONS SHOWING DEVELOPMENT OF NEURAL TUBE.

A, dorsal view of neural plate stage in human embryo Amnion partly removed. (Graf Spee, from Keibel and Mall.) A', diagram of portion of a transverse section of an embryo as though taken through A at the line a' B, dorsal view of human embryo of 7 somites in which neural tube is not yet closed (Dandy, from Keibel and Mall.) B', diagram to represent a transverse section of an embryo as though taken through B at the line b'. C', diagram to represent a transverse section of an embryo as though taken through C at the line c'. D, dorsal view of human embryo of 15 somites, neural tube closed save at caudal end. (Kollmann, from Keibel and Mall.) D', diagram to represent a transverse section of an embryo as though taken through D at the line d'. (human Anatomy, 9th ed, P. Blakiston's



shape in cross-sections of the cord in early stages. The lateral angles represent a longitudinal groove into the wall of the neural tube on each side known as the *sulcus limitans*. It divides the lateral wall into a dorsal sensory *alar plate* and a ventral motor *basal plate*. These form *longitudinal columns* (Figs. 6 and 8) which extend into the brain. The ventral floor of the neural tube, which remains thin, is called the *floor plate*. The roof is the *roof plate*. The floor

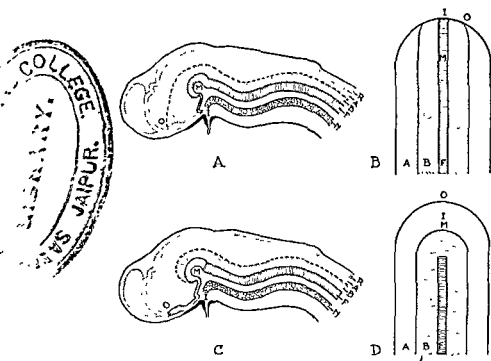


FIG. 6.—DIAGRAMS OF THE VERTEBRATE BRAIN TO SHOW THE FORWARD EXTENT OF FLOOR PLATE, BASAL PLATE, ALAR PLATE AND ROOF PLATE.

A, alar plate; B, basal plate; F, floor plate; I, primitive infundibulum; M, mammillary recess, N, notochord, O, preoptic recess; R, roof plate. A and B according to His, C and D according to Kingsbury

plate and roof plate are ependymal, but the lateral walls of the tube are made of neuroblasts, with an ependymal layer next to the ventricle.

The point of rostral termination of floor plate and basal plate is a question of much importance in interpretation of brain morphology. According to His the floor plate continues to the infundibular recess and the basal plate to the preoptic recess. The more recent studies of Kingsbury indicate that the floor plate ends at the fovea isthmi, at the posterior end of the midbrain, while the basal plate ends in the primitive infundibular recess at the rostral end of the midbrain (Fig. 6). According to this interpretation the motor column extends only into the midbrain, while the sensory alar plate is the foundation of the entire forebrain, including diencephalic and telencephalic structures.

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Two of the three primary brain vesicles each differentiates into two parts. The forebrain (prosencephalon) becomes divided into telencephalon and diencephalon. The hindbrain (rhombencephalon) divides into metencephalon (cerebellum and pons) and myelencephalon (medulla oblongata). The midbrain (mesencephalon) remains a unit. The result is five divisions of the brain which persist into the adult stage (Fig. 9). The further development of these divisions proceeds at very unequal rates of growth.

The neural cavity of the hindbrain region widens into the *fourth ventricle*. At its passage into the midbrain the neural cavity becomes constricted into the

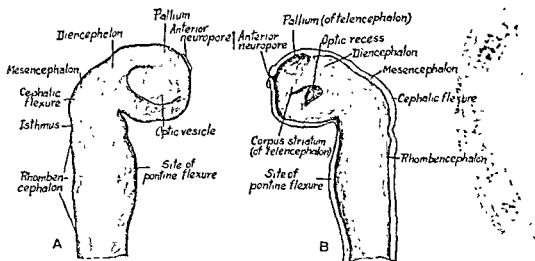


FIG 7—TWO VIEWS OF A HIS MODEL OF THE BRAIN OF A 3.2 MM. HUMAN EMBRYO.

A, surface view of right side; B, internal view of right wall. From Jordan and Kindred, *A Textbook of Embryology*, D. Appleton-Century Co., Inc., New York, 1937.

cerebral aqueduct or *aqueduct of Sylvius* In the diencephalon it enlarges into the cleft-like space of the third ventricle, which extends to the lamina terminalis, the rostral boundary of the telencephalon. Lateral continuations from the third ventricle extend into the cerebral hemispheres on each side as these are developed as rostral and lateral outpouchings of the telencephalon. The cavities of the hemispheres are the *lateral ventricles*. They remain connected with the third ventricle by the *interventricular foramina* (*foramina of Monro*).

The different rates at which the divisions of the brain grow at various periods, coupled with factors governing the development of the head, result in three flexures in the roof and floor of the brain. The *cephalic flexure* appears in embryos of about 3 mm. in the region of the midbrain. This is followed by a *cervical flexure* and subsequently by a *pontine flexure*. The cephalic flexure remains in the adult in reduced form, but the other two disappear with further growth of the brain.

The MYELENCEPHALON most closely resembles the spinal cord. In early stages a segmental arrangement is recognizable in this part of the brain in the form of six or seven *neuromeres*. The significance of these segment-like structures

shape in cross-sections of the cord in early stages. The lateral angles represent a longitudinal groove into the wall of the neural tube on each side known as the *sulcus limitans*. It divides the lateral wall into a dorsal sensory *alar plate* and a ventral motor *basal plate*. These form *longitudinal columns* (Figs. 6 and 8) which extend into the brain. The ventral floor of the neural tube, which remains thin, is called the *floor plate*. The roof is the *roof plate*. The floor

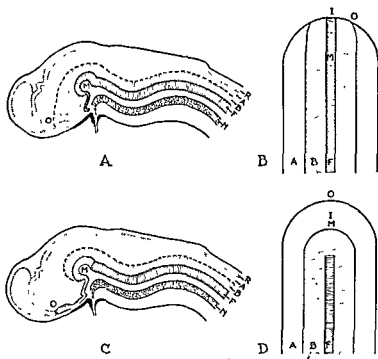


FIG. 6.—DIAGRAMS OF THE VERTEBRATE BRAIN TO SHOW THE FORWARD EXTENT OF FLOOR PLATE, BASAL PLATE, ALAR PLATE AND ROOF PLATE.

A, alar plate; B, basal plate; F, floor plate; I, primitive infundibulum; M, mammillary recess; N, notochord, O, preoptic recess; R, roof plate. A and B according to His, C and D according to Kingsbury.

plate and roof plate are ependymal, but the lateral walls of the tube are made of neuroblasts, with an ependymal layer next to the ventricle.

The point of rostral termination of floor plate and basal plate is a question of much importance in interpretation of brain morphology. According to His the floor plate continues to the infundibular recess and the basal plate to the preoptic recess. The more recent studies of Kingsbury indicate that the floor plate ends at the fovea isthmi, at the posterior end of the midbrain, while the basal plate ends in the primitive infundibular recess at the rostral end of the midbrain (Fig. 6). According to this interpretation the motor column extends only into the midbrain, while the sensory alar plate is the foundation of the entire forebrain, including diencephalic and telencephalic structures.

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of the rostral portion of this division. It arises as a bilateral structure which extends medially in the ependymal roof, to meet and fuse in the midplane. It is derived from the proprioceptive regions of the medulla oblongata. The pons develops on the underside of the myelencephalon as a mass of fibers and nuclei closely related functionally to the cerebellum.

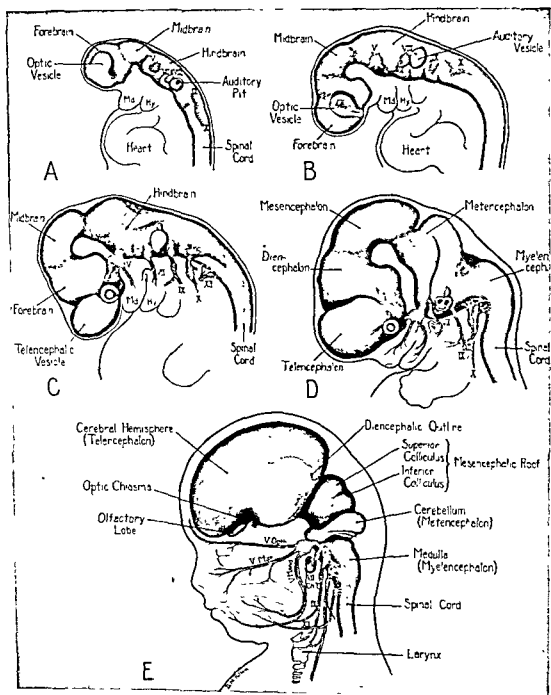


FIG. 9—STAGES IN DEVELOPMENT OF HUMAN BRAIN.

A, at 3 mm., B, at 4 mm., C, at 8 mm., D, at 7 weeks, E, at 3 months. From Arey, *Developmental Anatomy*, 3rd ed, W. B. Saunders & Co, Philadelphia, 1934. (After Patten.)

is a subject of disagreement among embryologists. According to some authors the neuromeres represent a primitive metamerism of the medulla oblongata corresponding to that of the spinal cord. Others regard them as transient features due to growth factors in the branchial region.

The nerves of the medulla oblongata do not show the typical dorsal and ventral roots seen in the spinal nerves. Two of them, the VIth and the XIIth, correspond to the anterior roots of the spinal nerves by reason of their position and the fact that they contain only motor fibers. The VIIth, IXth, Xth and

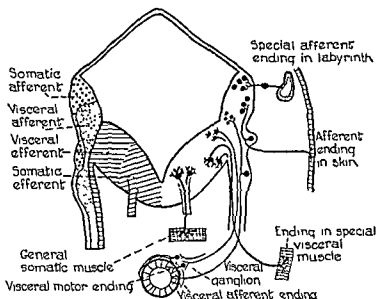


FIG. 8—DIAGRAMMATIC CROSS-SECTION THROUGH THE MEDULLA OBLONGATA AT LEVEL OF THE VAGUS NERVE.

This shows the four principal functional columns on left side, and the distribution of afferent and efferent fibers from these columns, including special somatic afferent fibers from the ear and special visceral efferent fibers to the branchial musculature. (After Herrick and Ranson.)

XIth nerves, however, emerge from the lateral surface of the medulla oblongata and have both sensory and motor fibers. Phylogenetically they are the nerves of the branchial arches.

The RHOMBENCEPHALON does not remain a tube like the spinal cord save at its lower end. The greater part becomes flattened into a shallow trough with gently sloping walls. The roof plate becomes greatly widened into the ependymal roof of the fourth ventricle. The alar plate has a lateral and slightly dorsal position and the basal plate has a ventromedial position. They are separated by the sulcus limitans, which in the medulla oblongata persists in the adult. The sensory nuclei of the bulb develop in the alar plate and the motor nuclei in the basal plate. Each plate is subdivided into somatic and visceral columns.

METENCEPHALON—Dorsal to the anterior part of the myelencephalon the cerebellum is developed as an upward growth of the rhombic lips and the floor

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cells, the *spongioblasts*, and to actively mitotic cells, the *germinal cells* of His (Fig. 10). The spongioblasts differentiate into ependymal cells and neuroglia, which become the connective tissue framework of the central nervous system. The germinal cells give rise to *neuroblasts*. The cellular basis of the nervous

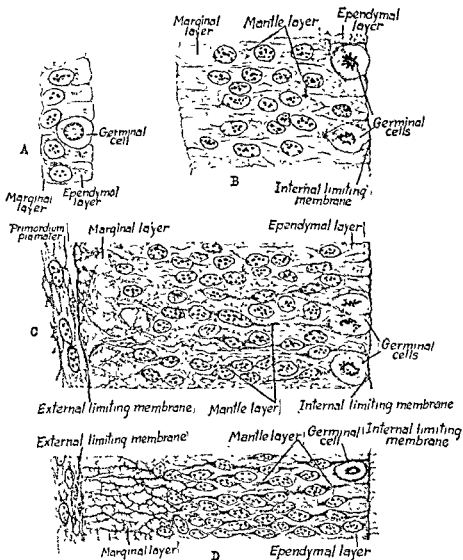


FIG 10—TRANSVERSE SECTIONS OF THE NEURAL TUBE ILLUSTRATING EARLY STAGES IN ITS HISTOGENESIS

.1, from rabbit embryo before closure of neural tube; B, from 5 mm pig embryo, just after closure of neural tube, C, from 7 mm. pig embryo; D, from 10 mm. pig embryo (After Hardesty, *Am J Anat*, 1904, Vol. 3.)

system, with the exception of one element of neuroglia known as microglia, is thus derived from ectoderm. The microglia is apparently derived from mesodermal cells which have migrated into the ectodermal mass, and form a special element of the connective tissue comparable to the histiocytes of connective tissue elsewhere.

MESENCEPHALON.—The midbrain remains tubular but its floor, walls and roof become greatly thickened by development of large nuclear masses. The basal plate shows the motor nuclei of the IIIrd and IVth nerves. The tegmentum also develops in the floor plate. The alar plate gives rise to the superior and inferior colliculi, receiving fibers from the retina and the cochlea, respectively. As the connecting part of the brain between cerebrum and myelencephalon, the ascending and descending paths pass through the midbrain in the cerebral peduncles.

The **DIENCEPHALON**, on the basis of Kingsbury's interpretation of brain morphology, has neither floor plate nor basal plate. The roof plate expands into a folded ependymal membrane in connection with which the chorioid plexus of the third ventricle is formed. The alar plate becomes greatly thickened. Three regions are formed, namely a dorsal *epithalamus*, an intermediate and lateral *thalamus*, and a ventral *hypothalamus*. The epithalamus includes a dorso-caudal outgrowth, the *pineal body* or *epiphysis*, which is now regarded as a gland whose function, however, is unknown. The nervous nuclei which develop in the epithalamus have to do with integration of somato-olfactory impulses. The thalamus becomes differentiated into a number of nuclei which are in part relay stations for chiefly somatic impulses, and in part correlation centers. The hypothalamus has to do with visceral reception and correlation. Attached by a stalk to the floor of the hypothalamus is the *hypophysis*, an important gland of internal secretion. It is derived, in part, from the floor of the embryonic diencephalon.

The **TELENCEPHALON** is formed entirely from the alar plate and the roof plate. As in the diencephalon the latter is expanded into ependymal folds connected with the extensive chorioid plexuses of the lateral ventricles. The rostral end, the *lamina terminalis*, of the forebrain vesicle remains as a morphological landmark between the two hemispheres, which are formed as outpouchings of the rostrolateral walls of the forebrain vesicle. The ventrolateral wall on each side thickens and differentiates into the nuclei, including the *caudate*, the *putamen* and the *globus pallidus*, which constitute the *striate body*. The remainder of the outgrowth becomes the pallium, which differentiates into *archipallium*, with olfactory connections, and *neopallium* which is nonolfactory. The *neopallium* becomes the predominant part of the brain in man.

NEURAL CREST.—As the neural tube is being pinched off from the overlying ectoderm, a ridge of cells (Fig. 5, C' and D') is formed on each side in the fold between the neural tube and the skin ectoderm. At first this is a continuous band, the *neural crest*. As development progresses it becomes segregated in each body segment into a pair of primordial ganglia, representing the incipient dorsal root ganglia in the region of the spinal cord and the sensory ganglia of the cranial nerves in the head region.

DIFFERENTIATION OF NEURAL TUBE.—The neural plate consists at first of generalized ectodermal epithelium. This gives rise to differentiated epithelial

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cells, the *spongioblasts*, and to actively mitotic cells, the *germinal cells* of His (Fig. 10). The spongioblasts differentiate into ependymal cells and neuroglia, which become the connective tissue framework of the central nervous system. The germinal cells give rise to *neuroblasts*. The cellular basis of the nervous

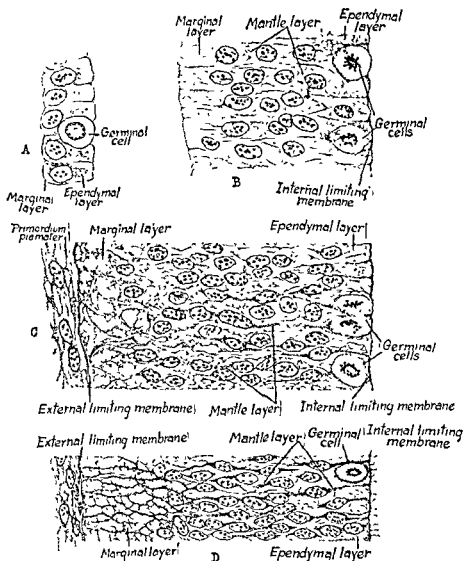


FIG 10—TRANSVERSE SECTIONS OF THE NEURAL TUBE ILLUSTRATING EARLY STAGES IN ITS HISTOGENESIS.

A, from rabbit embryo before closure of neural tube; *B*, from 5 mm pig embryo, just after closure of neural tube; *C*, from 7 mm. pig embryo; *D*, from 10 mm. pig embryo. (After Hardesty, *Am J. Anat.*, 1904, Vol. 3)

system, with the exception of one element of neuroglia known as microglia, is thus derived from ectoderm. The microglia is apparently derived from mesodermal cells which have migrated into the ectodermal mass, and form a special element of the connective tissue comparable to the histiocytes of connective tissue elsewhere.

The mitotic germinal cells are found between the outer ends of the resting epithelial cells in the neural plate stage. When the neural tube is formed the germinal cells retain their original position, but the outer surface of the plate has now become the inner surface of the tube. Mitotic figures and proliferation of cells are accordingly found bordering on the lumen of the neural tube. The cells resulting from this proliferative activity migrate away from the lumen, and as a result the wall of the tube becomes stratified.

Three layers may soon be seen in the tube wall (Fig. 10, B). The innermost is the *ependymal zone*, including the germinal cells. The cell bodies of this zone lie against the internal limiting membrane. The processes of the ependymal cells extend toward the outer surface of the tube. The germinal cells are ovoid or rounded cells without processes. The second layer is the *mantle zone*, made up of many layers of nuclei, the number increasing as the embryo grows. This zone is usually described as a syncytial mass of cytoplasm, but recent studies appear to confirm the earlier view of Ramón y Cajal that it is made up of distinct cells. It develops into the gray substance of the nervous system. The outer layer is the *marginal zone*, containing no cells. It eventually receives processes from neuroblasts of the spinal cord, the dorsal root ganglia and the brain. After a large proportion of these processes acquire myelin sheaths the embryonic marginal zone becomes the white substance of the nervous system.

Each *neuroblast* gives rise to a process (Fig. 11) at one end of the cell which by growth becomes the axon. It may attain a length of several feet in the cord and some of the long nerves before growth ceases. Dendritic processes arise from the opposite pole of the cell. In the simplest type of sensory neurons, the bipolar cells, the primitive condition of a process at each end of the cell is retained. In spinal and cranial ganglion cells, save those of the VIIIth nerve ganglia, the bipolar condition becomes modified by secondary growth of the cell and fusion of the proximal parts of the processes into the unipolar type. Multipolar cells are formed by expansion of the cell body into the bases of the dendritic branches or by outgrowth of more than one offshoot from the cell.

The processes of most of the cranial and dorsal root ganglion cells elongate into peripheral and central rami. They make up the sensory fibers of the cranial and spinal nerves. Some of the neuroblasts from the dorsal ganglia migrate ventralward and give rise to the sympathetic ganglia.

The ventral roots of the spinal nerves and the corresponding parts of cranial nerves are formed by axons of cells in the basal plate of the neural tube which grow outward. They meet the peripheral dorsal root processes and become enclosed in a sheath with them as the common nerve trunk.

In the ganglia of the spinal and cranial nerves the ectodermal connective tissue elements become differentiated into *capsule* or *satellite cells* and *sheath cells*. The satellite cells are flattened elements in a capsule which is formed about each ganglion cell. The sheath cells surround the processes of the nerve fibers, at first encircling bundles of fibers. With proliferation of sheath cells

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individual fibers are surrounded and the cells form a tube-like neurolemmal sheath about each fiber.

A *myelin sheath* is formed about many of the fibers of the central and the peripheral systems. In the latter the myelin sheath lies between the neurolemma and the axis cylinder. According to some accounts the myelin sheath is a product of the neurolemma cells, while others point to the axis cylinder as chiefly responsible for its formation. Sheath cells in the form of oligodendroglia are present in the central nervous system, but not in the tube-like arrangement characteristic of peripheral nerves. That the axis cylinder plays an important part in the maintenance of myelin, and therefore, probably, in its formation, is indicated

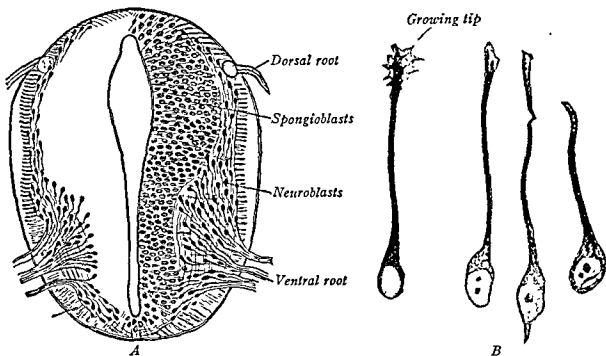


FIG 11—DEVELOPMENT OF NEUROBLASTS IN NEURAL TUBE.

A, transverse section of spinal cord of human embryo of five weeks, showing neuroblasts of ventral nerve root and spongioblasts (After His.) *B*, individual neuroblasts in chick embryo of three days, showing neurofibrils and growing tip (After Cajal.) From Arey, *Developmental Anatomy*, 3rd ed, W. B. Saunders & Co, Philadelphia, 1934.

by the fact that the myelin sheath degenerates if its nerve fiber is severed from the cell body. The degeneration takes place, primarily, distal to the point of injury.

The nervous system of mammals below man, and of lower vertebrates, shows various modifications of the fundamental plan of structure represented by the development of the brain in the embryo. The embryonic history is a sort of synopsis of the structural development of the nervous system from the lowest to the highest vertebrates. In fishes the brain-stem is present, together with a striate body in the forebrain. The pallium of the cerebrum is represented only by a non-nervous membrane. The beginning of cerebral cortex appears in the

amphibians as a thin layer of gray substance related to the olfactory centers. This archicortex becomes increased in reptiles and there appears the beginning of a neocortex. In lower mammals, like the marsupials, the archicortex is predominant, but the neocortex gains the ascendancy in development of the mammalian nervous system, and is predominant in man.

The cerebellum, which together with the cerebral cortex, is a suprasegmental structure, likewise undergoes great modification in its evolution from lower to higher vertebrates. In the lampreys it is present only as a commissural mass. In the good swimmers among the fishes, with a well coördinated muscular mechanism, the cerebellum is relatively large and well differentiated. In amphibians it is reduced, but in reptiles, birds and mammals it has undergone progressive enlargement and elaboration, reaching its highest development in man.

Many of the centers of the brain-stem undergo differing degrees of development in various types and species of vertebrates according to their habitat and sensory equipment. Thus the blind fishes of the Mammoth Cave have greatly reduced optic lobes in keeping with their lack of use of this nerve center. Man has greatly reduced olfactory centers corresponding to his reduced olfactory sensory equipment.

CHAPTER 3

STRUCTURAL ELEMENTS

THE NEURON

The neuron is the unit of structure of the nervous system. It consists of a cell body, the *perikaryon*, and a number of processes (Fig. 12). One type of process, called the dendrite, is a protoplasmic extension of the nerve cell which serves functionally to receive stimuli and to conduct them toward the perikaryon. Dendrites branch and spread out, as a rule, like the branches of a bush (dendron) from which they get their name. It is probable also, as was pointed out by Golgi, that dendrites serve as nutritive processes. A second type of process, called the *axon* or *neurite*, is a somewhat more specialized structure which serves to carry the impulse away from the perikaryon to another neuron or to an effector organ. The axon is a slender process of uniform diameter, which arises from a conical elevation of the perikaryon known as the *implantation cone* or *axon hillock*. This is free of Nissl substance. Axons have *collateral branches* which are given off at intervals. Structurally as well as functionally neurons, as a rule, show polarity. In some, as those of the dorsal root ganglia, there is no histological difference between the fibers which conduct toward the perikaryon and those which conduct away from it to the central nervous system. Developmentally these neurons undergo changes which convert the peripheral dendrite into a nerve process similar to the axon.

The PERIKARYON is characterized by a large vesicular nucleus and by granules of *chromophil substance* in the cytoplasm. This substance occurs as rounded granules 0.1 to 2 microns in diameter, but usually the granules are aggregated together as Nissl bodies. These are coarser in motor neurons than in sensory or correlative neurons. They extend into the dendritic processes but not into the axon. In living nerve cells the chromophil substance is not visible, a fact which has led some to consider the Nissl bodies as artefacts. Methods of technique, however, which rule out the possibility of precipitation due to reagents, show Nissl bodies in the same arrangement as do sections prepared by ordinary methods. Chemically the chromophilic substance is regarded by many authors as a nucleoprotein related to the chromatin of the nucleus. It is believed to contain iron and to store oxygen. The activity of the nerve cell is more or less explosive. This type of action, it is believed, is made possible by the organization of the chromophilic substance in such a manner that it is oxidized through-

out the nerve cell almost instantaneously. "Thus a very small stimulus may liberate a large amount of energy with explosive suddenness" (Herrick, 1927). Nissl bodies are affected by injury to the nerve cells or their processes. The chromophilic substance disintegrates and stains only diffusely or not at all by

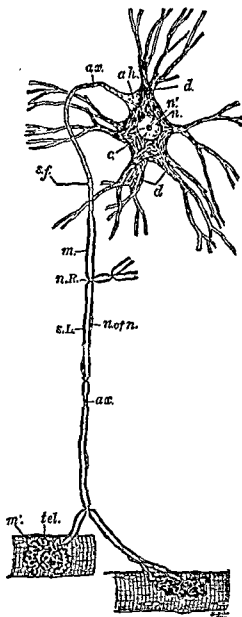


FIG. 12.—DIAGRAM OF A NEURON

ah, axon hillock; *ax*, axon; *c.*, cytoplasm, the Nissl granules have been stained; *d*, dendrons, *m.*, myelin sheath of the nerve fiber; *m'*, muscle fiber; *n.*, nucleus; *n'*, nucleolus; *n. of n.*, nucleus of the neurilemma of the nerve fiber; *n.R.*, node of Ranvier; *sf.*, collateral; *s.L.*, segment of Lantermann; *tel.*, telodendrion or terminal arborization which here forms a motor end-plate. (After Barker.) From Jordan, *A Textbook of Histology*, D. Appleton-Century Co., Inc., New York, 1937.

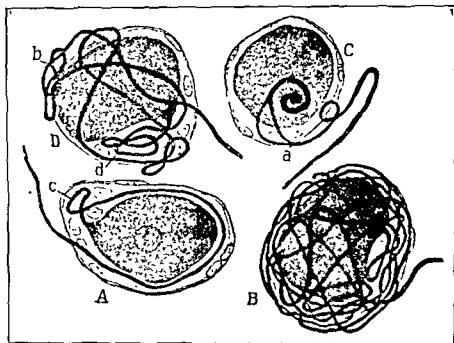


FIG. 13—SPINAL GANGLION CELLS.

Unipolar sensory ganglion cells, showing different types of arrangement of the fiber within the capsule. Cajal method. *A*, simple handle; *B*, capsule; *D*, satellite cells. From Cajal, *Histology*, Wm Wood & Co, Baltimore, 1933

the method of Nissl or its modifications. This is a fact of great importance to the experimental neurologist and the pathologist

Neurofibrillae.—These are delicate threads in dendrites, perikaryon, and axon which are made visible by certain methods of staining, as with silver nitrate and methylene blue (Fig. 20). They have been demonstrated by microdissection in living nerve fibers of invertebrates, but in the vertebrates this method has given negative results. Recently, however, they have been demonstrated in living ganglion cells of chick embryos. They form a complicated network within the cell body and extend to the finest branches of dendrites and axon. They have been described as passing into adjacent neurons at the synapse, but Bartelmez and Hoerr, and Bodian, especially, among many others, have shown that they are probably confined to one

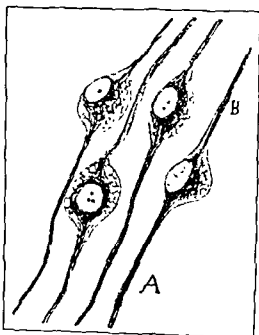


FIG. 14—BIPOLAR GANGLION CELLS FROM THE VESTIBULAR GANGLION OF SCARPA.

A, central process; *B*, peripheral process. Cajal method. From Cajal, *Histology*, Wm. Wood & Co., Baltimore, 1933.

neuron. Functionally they are regarded as the chief conductors, within the neuron, of the nervous impulse.

Nerve cells possess mitochondria, an internal reticular apparatus of Golgi, and in the embryo, while still capable of mitosis, they have a centrosome. In mammals proliferation of nerve cells appears to cease at about the time of

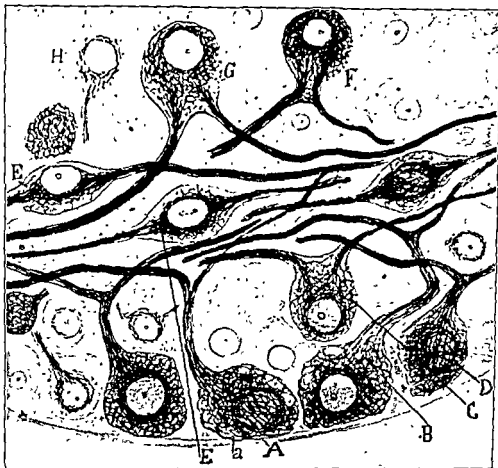


FIG. 15.—DEVELOPING SPINAL GANGLION CELLS.

A, B, unipolar cells, *E*, bipolar cell; *C, D, F, G*, transitional forms between the bipolar and the unipolar stages, *H*, small cell; *a*, neurofibrils. Cajal method. From Cajal, *Histology*, Wm Wood & Co, Baltimore, 1933.

birth and the centrosome disappears or becomes modified. Various other inclusions are found in the cytoplasm.

While nerve cells show a great variety of form, size and structure, according to their location and function, it is convenient to classify them into three main structural types, namely, *unipolar*, *bipolar* and *multipolar* (Figs. 13-21). Unipolar cells are found in dorsal root ganglia and ganglia of the cranial nerves. Bipolar cells are found, in adult mammals, only in the vestibular and cochlear

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ganglia. Multipolar cells are found throughout the central nervous system and in the sympathetic ganglia. The unipolar and bipolar cells are sensory nerve cells, the multipolar cells include all other functional types, both motor and correlating. They show a great variety of subtypes.

The **SYNAPSE** is the point of contact between nerve processes at which the

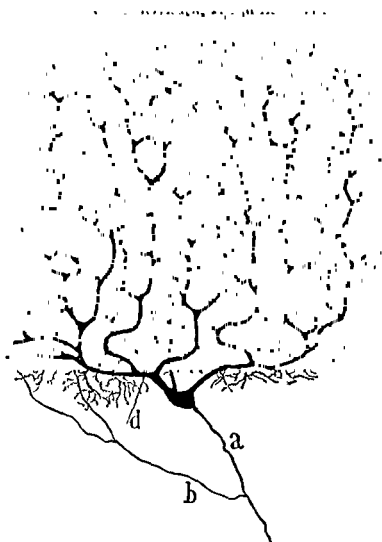


FIG. 16.—PURKINJE CELL OF HUMAN CEREBELLUM

a, axis cylinder; *b*, collateral from axis cylinder; *d*, spaces occupied by basket cells, Golgi method From Cajal, *Histology*, Wm Wood & Co, Baltimore, 1933

nervous impulse is transmitted from one neuron to another. There are many types of synaptic connection, from simple, club-like swellings (Fig. 25) at the ends of nerve fibers, known as *boutons terminaux*, to complex pericellular baskets on the surface of cell body or dendrite. Recent studies indicate that there is a membrane at the synapse (Fig 26) which the neurofibrils do not

bridge. The membrane is made up of the superficial cytoplasm of the two related neurons. The two sides of the membrane are unlike in structure and in functional properties.

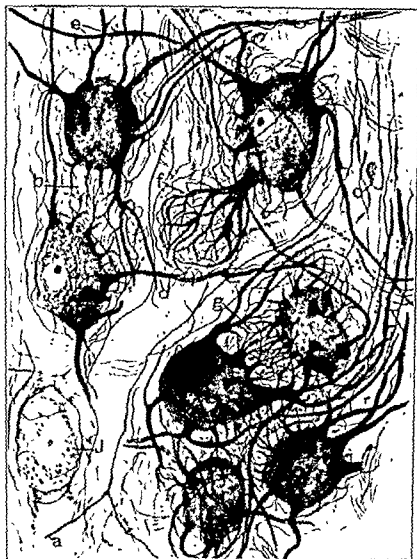


FIG 17.—SYMPATHETIC GANGLION CELLS.

a, branched afferent fiber; *b*, accessory dendrites; *d*, long dendrite terminating among accessory dendrites of another cell; *f*, pericellular dendritic nest; *g*, networks of accessory dendrites. (After Castro) From Cajal, *Histology*, Wm. Wood & Co, Baltimore, 1933.

THE NEURON DOCTRINE—Nerve cells and fibers constitute the functional elements of the nervous system. The studies of His (1889), Harrison (1907), and others have demonstrated that the nerve cell is an embryological unit from which the nerve fibers grow out as processes of protoplasm. The older conception of Balfour that nerve fibers are formed in the tissues and become

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united to the nerve cells secondarily is no longer held. Likewise the conception of Donders that the nerve fibers form a reticulum within the central nervous system has been discarded. In 1891 Waldeyer formulated the accumulated embryological, pathological, physiological, and other evidence regarding the individuality of the nerve cell into the neuron doctrine. As modified, this doctrine now holds, briefly, that the neuron is the unit of structure of the nervous system, and also the ultimate functional unit. Nerve fibers are regarded



FIG 18 A—GOLGI CELL, TYPE I.

c, collaterals, n, axon Golgi's stain. (After Kolliker) From Jordan, *A Textbook of Histology*, D Appleton-Century Co, Inc., New York, 1937.

as specialized protoplasmic processes of the nerve cell, but are integral parts of the neuron. The neuron therefore consists of a cell body, or perikaryon, together with dendrites and their branches, the axon and its collaterals, and the terminal or synaptic processes of dendrites and axon.

NERVE FIBERS are classified into myelinated (Fig. 24) and unmyelinated, each type being further subdivided according to whether or not the fibers have a neurolemma. There are thus four structural types. The essential feature of all is the axis cylinder, which may be an axon or the peripheral (embryologically,

dendritic) process in the case of sensory neurons. Myelinated, as well as unmyelinated fibers possessing a neurolemma, together with some naked nerve fibers, are found in the peripheral nerves and the sympathetic system. Myelinated fibers with no neurolemma, together with unmyelinated fibers also without neurolemma, are characteristic of the central nervous system. The sheathis

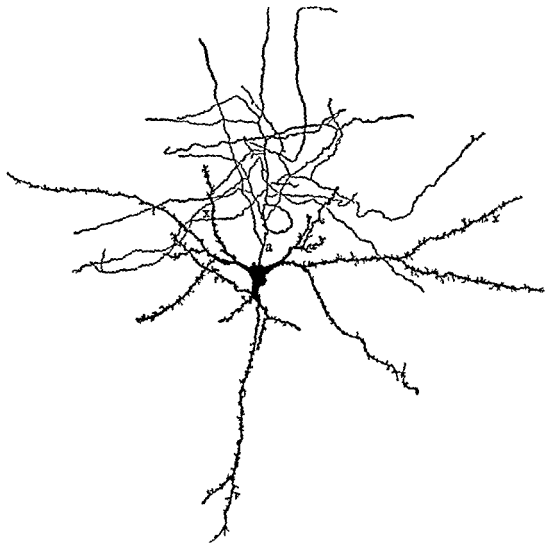


FIG 18 B.—GOLGI NERVE CELL, TYPE II.

x, axon; d, dendrite. (After Kölliker) From Jordan, *A Textbook of Histology*. D. Appleton-Century Co., Inc., New York, 1937

are not continuous throughout the length of the nerve fibers. The myelin sheath undergoes degeneration in the distal part of myelinated nerve fibers which have been severed. Due to chemical changes it is possible to stain such degenerating fibers differentially (by the Marchi osmic acid method). This fact is of great importance in the study of the nervous system.

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Nerve fibers usually are found in bundles save near their terminations. Within the central nervous system the bundles constitute fiber tracts and are usually made up of aggregations of the same functional type, passing from

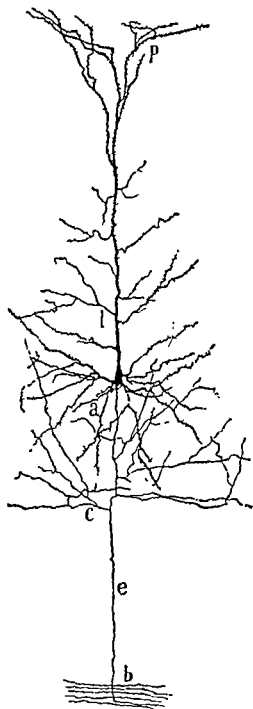


FIG 19—PYRAMIDAL CELL OF CEREBRUM OF RABBIT.

Type of cell with long axon, *a*, basilar dendrites; *b*, apical dendrite and branches (*p*), *c*, collaterals of axon; *e*, axon; *l*, white substance of brain, *p*, telodendrites of apical dendritic process. Golgi method. From Cajal, *Histology*, Wm. Wood & Co, Baltimore, 1933

one part of the nervous system to another. In the peripheral nerves the bundles are composed of many functional types of fibers, since these nerves serve as trunks of distribution of the various kinds of sensory fibers to their segmental skin areas, and also distribute motor fibers to the muscles at various levels. By the sympathetic trunk, which is connected with the spinal nerves, and its

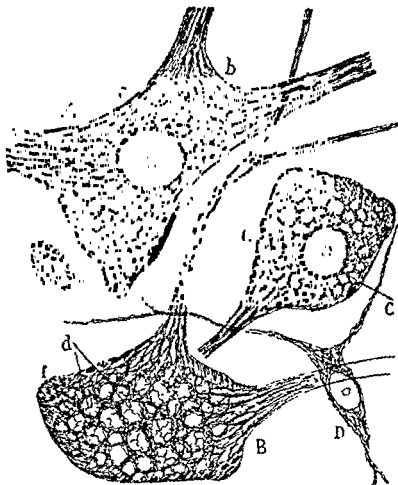


FIG. 20.—NERVE CELLS SHOWING NEUROFIBRILLAE.

A, equatorial plane; *B*, superficial plane, *a*, *b*, superficial bundles of neurofibrillae; *c*, perinuclear plexus of neurofibrillae; *d*, spaces occupied of Nissl granules, surrounded by fine network of neurofibrillae, *D*, small nerve cell. From Cajal, *Histology*, Wm Wood & Co, Baltimore, 1933

branches, both afferent and efferent fibers also are distributed to the viscera and the blood vessels.

Peripheral nerve trunks (Figs. 32 and 33) are formed by the converging of individual fibers from areas of skin and from the individual fibers of muscle to form small bundles. These unite with similar bundles to form larger ones, the smaller bundles becoming encased in a common sheath of connective tissue. These in turn become encased within a common sheath of epineurium with

other bundles, until there results the final main nerve trunk attached to the spinal cord or to the brain stem. The larger nerves are made up, as seen in

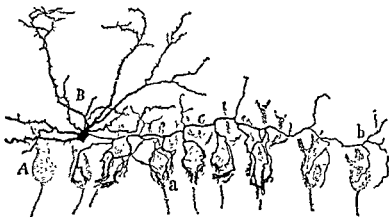


FIG. 21—BASKET CELL OF CEREBELLUM OF RAT. GOLGI METHOD

From C J Herrick (after Cajal), *Introduction to Neurology*, 5th ed, W. B Saunders & Co, Philadelphia, 1931.

cross-section (Fig. 32) of bundles of fibers, known as *funiculi*. Each is surrounded by a definite sheath of connective tissue, the *perineurium*. Within each funiculus there is a network of delicate strands of connective tissue, the *endoneurium*, binding the fibers together. It is continuous with the perineurium of the funiculus.

The functional types of fibers composing a nerve vary with the part of the nerve examined. The cutaneous nerves are composed entirely of somatic afferent fibers serving sensory terminations in the skin, together with some visceral efferent fibers to sweat glands, cutaneous blood vessels, and the muscles of the hairs. The afferent fibers carry several types of stimuli, as e.g., touch, pressure, heat, cold, etc. It is usually thought that each type of stimulus has its specific nerve ending. Woollard

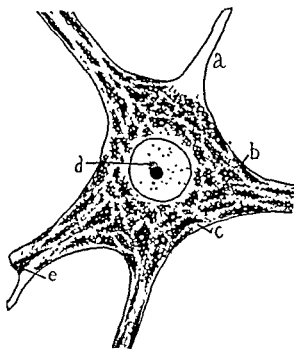


FIG. 22—MOTOR NERVE CELL SHOWING NISSL GRANULES.

a, axis-cylinder; *b*, Nissl bodies; *d*, nucleus; *c*, spongoplasm; *e*, mass of Nissl substance at division of dendrite. (Thionin stain.)

has demonstrated separate receptors for pain and cold. Probably each has its separate nerve fiber but this point has not been established. It must be recognized that different types of nerve endings may send impulses through common



FIG. 23 — MYELINATED NERVE FIBERS.

a, node of Ranvier, b, intersegmental cement disc, blackened by silver nitrate; d, axon; f, g, nuclei of neurolemma cells, e, Schmidt-Lantermann segment. Cajal, *Histology*, Wm. Wood & Co

nerve fibers. The segregation of specific fiber tracts in the cord suggests that the functional fibers are specific.

The muscular nerves are made of motor fibers terminating in *motor end plates* on individual striated muscle fibers, together with afferent *proprioceptive fibers*. The latter terminate as *neuromuscular* or *neurotendinous spindles*. When activated by muscular movement these endings give rise to stimuli of muscle sense which give information, frequently not coming to consciousness, of the position and stretch of muscles and joints, thus coördinating muscular movement through their central connections.

The processes of nerve cells vary in length. Golgi made a classification of Types I and II, according to the length and distribution of the axons of cells in the central nervous system. Golgi cells of Type I have long axons with few collaterals and are adapted for rapid transmissions of stimuli for considerable distances. Golgi cells of Type II have short axons with many branches which terminate near the cell from which they originate. There are many intermediate forms of cells. The axons of some neurons attain a length of several feet in man, as for example, the upper motor neurons of the corticospinal tracts. In this case the cell bodies (Betz cells) are located in the precentral gyrus of the cortex, while the terminal processes of many of these cells extend to the lumbosacral region of the spinal cord. Likewise the peripheral processes of spinal ganglion cells supplying skin areas of the hand and foot, for example, extend from the nerve endings in the skin of these parts to the dorsal root ganglia of the lower cervical or upper thoracic nerves, in the one case, or to the corresponding ganglia of the sacral nerves in the other. The size of the perikaryon also varies from a diameter of four microns, for the granule cells of the cerebellum, to a diameter of about 80 microns in the case of ventral horn cells of the cord.

NEUROGLIA

The specific functional elements of the nervous system are the nerve cells and their processes, but these are held in place and aided in their function by another element called neuroglia. This may be considered, in general, as the connective tissue of the nervous system. Like the latter it is derived, with the exception of the microglia cells, to be described, from

STRUCTURAL ELEMENTS

the ectoderm. Ordinary connective tissue of mesodermal origin is widely distributed, in the central nervous system, in the sheaths of the blood vessels, forming with the vessels the main beams of support. Mesodermal connective tissue also constitutes the major part of the meningeal membranes and the coverings

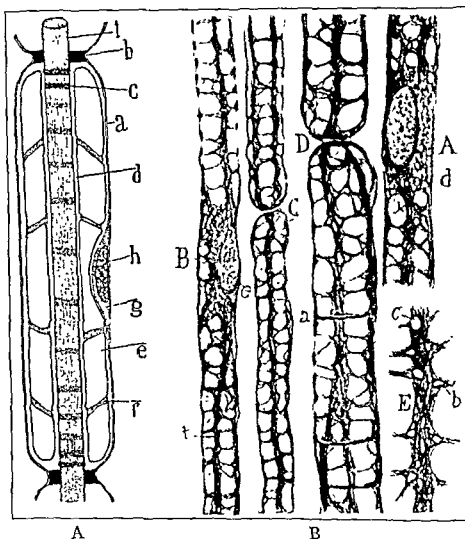


FIG 24.—DIAGRAM OF MYELINATED NERVE FIBERS.

A, *a*, sheath of Schwann; *b*, node of Ranvier; *c*, lines of Frommann; *e*, myelin; *f*, incisures of Lantermann, *h*, nucleus of neurolemma cell; *g*, cytoplasm of neurolemma cell; *i*, axis cylinder

B, *d* and *B*, protoplasm of sheath cells; *D*, *C*, nodes of Ranvier; *a*, incisures of Lantermann showing hooplike structure, *b*, *c*, vacuoles, *e*, nucleus of neurolemma cell; *t*, longitudinal bands; *E*, longitudinal band greatly magnified. From Cajal, *Histology*, Wm. Wood & Co., Baltimore, 1933.

of the peripheral nerves, save the neurolemma. The neuroglia, however, is the principal connective tissue element both of the brain itself and of the spinal cord.

In the broad sense neuroglia may be regarded as including the *ependymal*

cells of the adult, the *astrocytes*, *oligodendrocytes*, and *microglia* of the central nervous system, the *satellite* or *capsule cells* of peripheral ganglia (dorsal root and sympathetic) and the *neurolemma cells* or *cells of the sheath of Schwann* of peripheral nerves. These are all derived from ectoderm. The microglia cells, mentioned above, are also included with neuroglia, but are derived from mesoderm.

A clear picture of the neuroglial elements can best be obtained by considering briefly their histogenesis. The neural plate of the embryo early is made

up of epithelial cells of ectodermal origin. These give rise to *spongioblasts* and *germinal cells*. The spongioblasts are differentiated epithelial cells, which by further differentiation give rise to various types of neuroglia cells (Fig. 27). The germinal cells proliferate by mitosis and give rise chiefly to neuroblasts, but some may form spongioblasts. According to Schaper some of the germinal cells retain the potentiality of forming neuroblasts or spongioblasts for a considerable time. The spongioblasts of early development assume a pseudostratified appearance by migration of some of the nuclei away from the border of the central canal or ventricle toward the periphery. They also send processes to the surface which terminate as small expansions at the external limiting membrane of the nerve tube. The inner end of the cell lies against the inner limiting membrane. This end develops cilia, which remain, in parts of the nervous system, into adult life. Some of the spongioblasts migrate outward. With increasing thickness of the medullary wall, they may lose their contact with the inner limiting membrane. These



FIG 25—NERVE CELL SHOWING
TERMINAL CLUBS PYRIDINE SIL-
VER METHOD.

become the *astroblasts* of *Lenhossék*. Some also lose their connection with the pia and become *astrocytes*. Those which retain their pial contact form the *subpial neuroglia*. In the cerebellum very long pial processes are retained by the astrocytes, constituting the *fibers of Bergmann*. From the third month and later, in human development, the spongioblasts which migrate into the wall of the nerve tube from the ependymal epithelium give off processes which tend to become attached to blood vessels, thus obtaining anchorage. The processes of other neuroglial elements interlacing with the free processes of the anchored

cells result in a special connective tissue bed in which the nerve cells and fibers are maintained in place.

Four main types of neuroglial elements are usually recognized in the adult, namely, ependymal cells, astrocytes, oligodendrocytes, and microgliaocytes.

EPENDYMAL cells are the modified epithelial cells (Fig. 28) which line the central canal of the cord and the ventricles of the brain. Wherever the wall of the nerve tube remains relatively thin in the adult, as at the ventral fissure of the cord and the median raphe of the hind brain, the peripheral processes continue to the pia mater and attach to the latter by a pial foot. In the thicker walled portions of the central nervous system the peripheral processes of the

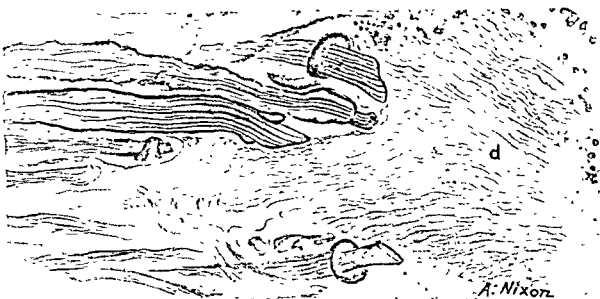


FIG. 26—SEVERAL LARGE MYELINATED VESTIBULAR FIBERS ENDING BY MEANS OF CLUB-SHAPED TERMINALS ON LATERAL DENDRITE (d) OF MAUTHNER'S CELL.

Note arrangement of neurofibrils in axons and in dendrite, and the difference in the caliber. Dendrite cut obliquely. From D. Bodian, *J. Comp. Neurol.*, 1937, 68:147.

ependymal cells merely extend a greater or less distance into the brain or cord substance. In thin or non-nervous parts of the brain, as the epithelial layer of the chorioid plexus, the ependyma retains its simple epithelial structure in the adult. Neuroglia has been described as a reticular syncytium, but newer methods of technique show individual cells, both embryologically and in the adult.

ASTROCYTES or MACROGLIA (Fig. 29) are stellate cells subdivided into *fibrous* and *protoplasmic* astrocytes. The latter type has protoplasmic processes which branch freely in all directions. Some of these processes have perivascular feet by means of which the cells are anchored to blood vessels. The protoplasmic processes surround nerve cells and fibers. The *fibrous* astrocytes have fibers

in the protoplasm of the processes and extending through the cell bodies. The processes do not branch as freely as in the protoplasmic type. As in the latter type one or more of the processes are anchored by perivascular feet to blood vessels within the nervous substance.

As subtypes of astrocytes there are: (1) *perivascular astrocytes* whose fibers form a meshwork about the blood vessels, chiefly the larger ones; (2) *marginal glia cells*, just under the pia mater of the cerebrum, whose fibers extend parallel

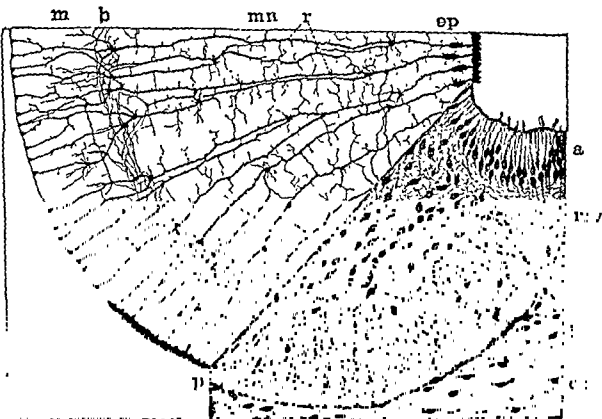


FIG. 27.—NEUROGLIA FROM THE SPINAL CORD OF A FETAL PIG.

The portion above shows the result of the Golgi stain; below, that of a hematin and Congo red stain. *a*, inner layer of neuroglia, adjoining the central canal; *b*, boundary between the nucleated and mantle layers of neuroglia; *cs*, connective tissue; *ep*, ependyma; *m*, mantle layer; *mn*, middle or nucleated layer of neuroglia; *mc*, ventral raphe; *p*, pia mater; *r*, radial filaments of the neuroglia. X320 (After Hardesty) From Jordan, *A Textbook of Histology*, D. Appleton-Century Co., Inc., New York, 1937.

to the pia and into the brain substance. These cells have pial feet of attachment and may have perivascular feet. (3) a third subtype is the *subpial astrocyte*, characteristic of the cerebellum. The cell bodies lie in the granular layer of cerebellar cortex, but give off long, straight processes, the *fibers of Bergmann*, which attach by terminal feet to the pia; (4) *satellite astrocytes* of Cajal lie close to nerve cells and have protoplasmic processes surrounding the latter; (5) *mixed type astrocytes* of Cajal have both protoplasmic and fibrous processes.

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OLIGODENDROGLIA (Fig. 29) have few and small processes without fibers and without perivascular feet. The cell body is smaller than that of astrocytes. There are three main subtypes, namely, (1) *perineuronal satellites*, (2) *perivascular satellites*, and (3) *interfascicular glia*. The latter is characteristic of the white matter of the central nervous system, the cells occurring in rows between the myelinated nerve fibers, with occasional astrocytes and microcytes interspersed. The processes of these cells wrap about the myelinated fibers, forming a loose network. The perivascular satellites have their cells attached

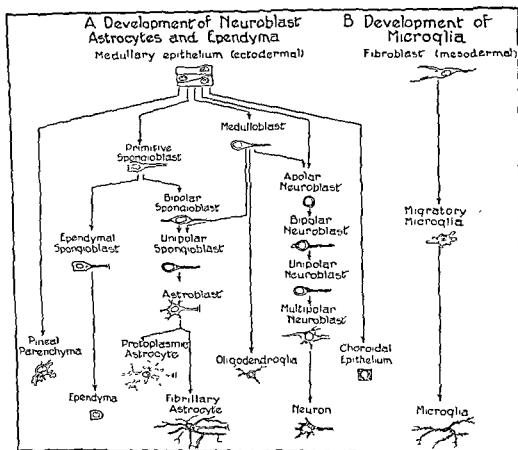


FIG. 28.—DEVELOPMENT OF NEUROGLIA.
 (Redrawn in part after Bailey)

to capillaries in both gray and white matter, while their processes extend into the surrounding field. Perineuronal satellites of this group give off processes which surround the nerve cells and continue into the surrounding field.

Oligodendroglia cells appear to have a part in the formation of myelin in brain and cord, serving the function here which the *neurolemma* cells serve in peripheral nerves. The perineuronal satellites of this group are regarded as similar to the capsular cells of spinal ganglia. Oligodendroglia appears to serve a nutritional function for the neurons, rather than a supporting function.

In the peripheral nerves the cells of the sheath of Schwann and the capsular

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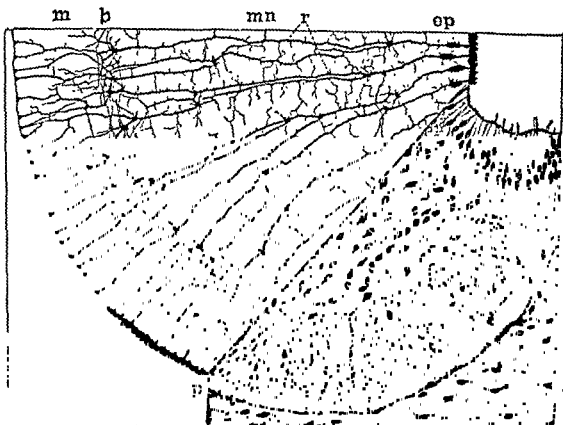


FIG. 27.—NEUROGLIA FROM THE SPINAL CORD OF A FETAL PIG.

rec
sub
layer; *mn*, middle or nucleated layer of neuroglia; *mn*, ventral raphe; *p*, pia mater; *r*, radial filaments of the neuroglia. X320 (After Hardesty) From Jordan, *A Textbook of Histology*, D. Appleton-Century Co., Inc., New York, 1937.

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or satellite cells of spinal, and probably of sympathetic ganglia, are of ectodermal origin. It is likely that they correspond functionally to oligodendroglia of the brain and cord. The sheath of Schwann is regarded as indispensable in the formation of myelin in peripheral nerve fibers. The capsular or satellite cells are held to serve a nutrient function for the ganglion cells.

MICROGLIA OR MESOGLIA OF HORTEGA (Figs. 28 and 29) was included by Ramón y Cajal with oligodendroglia as his third element of the central nervous system. It is now recognized that microglia is derived from the mesoderm, thus having an origin different from nerve cells and the other types of neuroglia. The cells are small, with elongated or triangular nuclei. The cytoplasm is finely granular and has delicate processes with small terminal spines. Fibers and perivascular feet are absent. The cells are scattered throughout the central nervous system and are more numerous in the gray matter than in the white. There are two subtypes, namely, (1) *perivascular satellites*, and (2) *perineuronal satellites*, distinguished from the oligodendroglia cells of the same names by their cytoplasmic and nuclear characteristics, and by their processes.

Microglia is now regarded, functionally, as part of the reticuloendothelial system. The cells have capacity for active movement, phagocytic activity and transportation of materials. They are the only cells of the nervous system in which these functions have been demonstrated. Microglia is recognized as having great significance in many pathological conditions of the central nervous system.

Functionally the different types of neuroglia appear to be fairly distinct. Ependymal cells, in the adult, form the lining of the ventricles and the central canal. The cells, with their nuclei, form a relatively thick internal limiting membrane from which branching protoplasmic processes extend into the thick walls of brain and cord. These processes interlace with each other and with processes of astrocytes and other neuroglial elements. The ependyma can therefore be regarded as a sort of foundation upon which the other supporting elements of the neuroglia are superimposed. In the embryo, and so far as the cells retain cilia, in the adult, the movement of the cilia probably aids in the flow of cerebrospinal fluid in the ventricles and central canal.

Because of their attachments to pia mater and blood vessels within the central nervous system, and because of their fibers, astrocytes are regarded as the connective tissue proper of brain and cord, supporting and binding together the nervous elements. It has been suggested that astrocytes constitute a gland of internal secretion; also that by contraction of their processes they may affect the synaptic connections between neurons.

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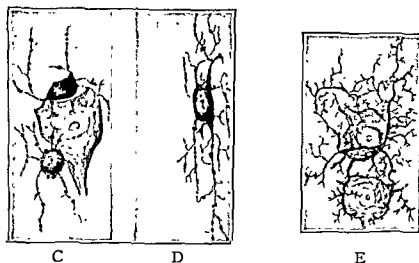
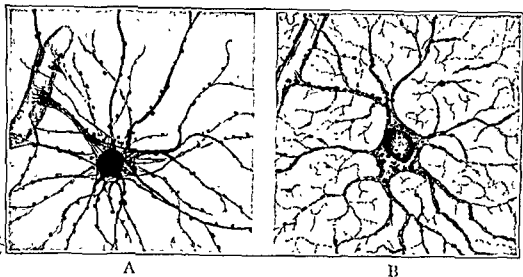


FIG 29—TYPES OF NEUROGLIA

A, fibrous astrocytes, with processes ending as perivascular feet on a blood vessel and other processes ramifying into the nervous tissue. *B*, protoplasmic astrocyte, with perivascular feet at tips of some of the processes, and other processes branching freely. Gliosomes are present as granules both in the cell bodies and in the processes of both types of astrocytes. *C*, satellite oligodendroglia cells in relation to a nerve cell, occurring in the gray substance, of brain and cord. *D*, inter fascicular oligodendroglia cell occurring in the white substance of the central nervous system. *E*, microglia cell in relation to two nerve cells. (From Jordan, after Penfield and Cone.)

CHAPTER 4

METHODS OF STUDYING THE NERVOUS SYSTEM

The results obtained by investigators of the nervous system are more readily understood if the student has some knowledge of the methods employed. These methods may be grouped as anatomic, physiologic, and pathologic, each supplementing the other. The anatomic method may be subdivided into comparative, microscopic and experimental. The physiologic method is both comparative and experimental. The pathologic method seeks to gain knowledge of structure and function of different parts of the nervous system by checking pathologic lesions in the nervous system with careful clinical histories taken prior to death of the patient studied. It involves both gross and microscopic anatomy.

THE METHOD OF COMPARATIVE ANATOMY

The comparative anatomical method is based on the study of the nervous systems of animals with different habits and various combinations of sensory equipment. For example, the cat fish, *Amieurus*, has a greatly enlarged system of taste buds, found not only in the mouth, but on barblets extending from the surface of the head. It has been found that the brain centers to which the gustatory fibers pass are also larger than corresponding parts of the brains of other fishes with a less developed peripheral gustatory apparatus. The inference is justified that the central nuclei involved are concerned with gustatory reflexes. Since the brain-stem of man has the same structural pattern as that of fishes, as comparative studies have also shown, the inference is justified that the corresponding nuclei in man and mammals also are gustatory. Experimental studies have confirmed this inference.

Another valuable feature of the comparative method lies in the fact that the nervous system of lower vertebrates is, as a rule, less complex than that of man. Yet the fundamental pattern has been found to be the same. Detailed microscopic studies of lower forms thus may provide paradigms upon which an understanding of the more complex pattern may be based. They also serve as a basis for experimentation on more complex nervous systems. Many of the fundamental facts and concepts of neurology have been obtained by the comparative method.

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affinity of nerve cells and fibers in the living condition for methylene blue. Surrounding tissues are shown very lightly stained or not stained at all. It is thus possible to follow nerve processes for long distances in whole mounts or thick sections of tissue. Various modifications of the methylene blue technique have also given valuable information about details of structure of cells and fibers. The methylene blue technique has been especially valuable in the study of nerve terminations.

THE NISSL METHOD.—Methylene blue can be used to stain fixed material. The modification devised by Nissl, in its various adaptations, has been of great value in localizing nuclear masses, as well as in the study of cell types. The stain has a special affinity for the Nissl granules or tigroid substance in nerve cells. This substance undergoes chromatolysis when nerve cells or their processes are injured. The chromatolysis requires about two weeks for completion in mammals. Experimental lesions affecting fiber tracts, followed by use of the Nissl method on the nerve centers on animals killed after an interval sufficient for chromatolysis to be accomplished, has yielded most important information as to the relation between fiber tracts and central nuclei.

THE WEIGERT METHOD stains myelinated nerve fibers only. It depends on the fact that nervous tissue, fixed in potassium dichromate, retains the myelin of myelinated fibers when subsequently passed through the fatty solvents such as alcohol, xylol, etc., which are usually employed in preparation of sections of tissue. When copper sulphate is added to the solution a mordanting action occurs which makes the myelin stainable by hematoxylin. Normal myelinated fibers and fiber tracts can be stained selectively by this method, which has been invaluable in mapping out the course of nerve fiber bundles. The *Pal-Weigert* method is a modification usable after fixation in formalin.

Flechsig, applying the Weigert method on the central nervous system of fetuses of four months and later, has worked out the sequence of myelination of many of the fiber tracts. Because different tracts acquire their myelin sheaths at different stages of fetal development, he has been able to trace the course of the tracts and has added greatly to our knowledge of their origins and terminations.

THE MARCHI METHOD.—It was shown by Waller in 1853 that severed nerve fibers undergo degeneration (wallerian degeneration) distal to the level of section. It is now known that this is due to cutting off the distal part of the fiber from its trophic center, the cell body. The degeneration of the axis cylinder is accompanied or followed by degeneration of the myelin sheaths. The latter undergo chemical changes which make the fatty substances, after a proper interval, reduce osmic acid if the tissue has previously been fixed in potassium dichromate. The droplets of myelin of the degenerated fibers become blackened by the osmic acid, while the surrounding normal nervous tissue has a yellowish color. It therefore is easy to follow the course of degenerated fiber tracts in serial sections. The Marchi method has many pitfalls but is indis-

HISTOLOGIC METHODS

Microscopic study of the nervous system involves special techniques for the staining or impregnation of the various tissue elements which form the brain, spinal cord and nerves. Nerve cells and fibers, as well as neuroglia, may be stained by ordinary histologic methods, but special methods have been found necessary for revealing the processes of nervous tissue. These methods have yielded a wealth of information. They may be described as impregnation methods and staining methods.

IMPREGNATION METHODS.—Gold chloride in solution, acting on nerve cells or fibers, properly prepared as by previous immersion in lemon juice or formic acid, will, when exposed to light, form a precipitate on the nervous tissue which differentiates the latter from other tissues. The precipitating action can be stopped at the desired point by immersing the tissue again in the acid. The stained tissue may be mounted in glycerine or glycerine jelly. The method is of value for nerve endings, but does not afford much histological detail.

THE GOLGI METHOD.—In 1873 it was announced by Golgi that pieces of the central nervous system previously saturated for a considerable period in potassium dichromate solution, when placed in a solution of silver nitrate, acquire a black impregnation on some of the nerve cells and their processes. Not all of the cells are stained, a point of great value in view of the numerous processes possessed by neurons. It is therefore possible to follow the various branches of individual cells for long distances in thick sections. The Golgi method and its modifications, involving the use of osmic acid with the potassium dichromate, thereby hastening the action, have yielded some of the most important facts in our knowledge of the types of nerve cells and their connections.

The **REDUCED SILVER NITRATE METHOD** of Ramón y Cajal has as its basis the fact that nervous tissue, properly prepared by fixation beforehand in certain mixtures of fluids, has a selective affinity for silver nitrate. By employing a reducing reagent such as pyrogalllic acid or hydroquinone, the non-nervous tissues remain yellowish in color while nerve cells and fibers acquire a brown to black color. The nerve processes and cells can thus readily be distinguished and studied in sections. Many important details of the finer structure of nervous elements have been obtained by this method.

The **PYRIDINE-SILVER METHOD** of Ranson is a modification of the method of Ramón y Cajal. It involves treating the tissue with pyridine after fixation in ammoniated alcohol. The tissue is then treated with silver nitrate for some days, placed into a reducing mixture, and prepared for sectioning. A number of modifications of the reduced silver nitrate methods designed for staining sections instead of blocks of tissue have been devised by Bielschowsky, Rogers, Davenport and Bodian.

The **INTRAVITAM METHYLENE BLUE METHOD**, first elaborated by Ehrlich and improved for nervous tissue by Dogiel and Bethe, depends upon the selective

affinity of nerve cells and fibers in the living condition for methylene blue. Surrounding tissues are shown very lightly stained or not stained at all. It is thus possible to follow nerve processes for long distances in whole mounts or thick sections of tissue. Various modifications of the methylene blue technique have also given valuable information about details of structure of cells and fibers. The methylene blue technique has been especially valuable in the study of nerve terminations.

THE NISSL METHOD.—Methylene blue can be used to stain fixed material. The modification devised by Nissl, in its various adaptations, has been of great value in localizing nuclear masses, as well as in the study of cell types. The stain has a special affinity for the Nissl granules or tigroid substance in nerve cells. This substance undergoes chromatolysis when nerve cells or their processes are injured. The chromatolysis requires about two weeks for completion in mammals. Experimental lesions affecting fiber tracts, followed by use of the Nissl method on the nerve centers on animals killed after an interval sufficient for chromatolysis to be accomplished, has yielded most important information as to the relation between fiber tracts and central nuclei.

THE WEIGERT METHOD stains myelinated nerve fibers only. It depends on the fact that nervous tissue, fixed in potassium dichromate, retains the myelin of myelinated fibers when subsequently passed through the fatty solvents such as alcohol, xylol, etc., which are usually employed in preparation of sections of tissue. When copper sulphate is added to the solution a mordanting action occurs which makes the myelin stainable by hematoxylin. Normal myelinated fibers and fiber tracts can be stained selectively by this method, which has been invaluable in mapping out the course of nerve fiber bundles. The *Pal-Weigert* method is a modification usable after fixation in formalin.

Flechsig, applying the Weigert method on the central nervous system of fetuses of four months and later, has worked out the sequence of myelination of many of the fiber tracts. Because different tracts acquire their myelin sheaths at different stages of fetal development, he has been able to trace the course of the tracts and has added greatly to our knowledge of their origins and terminations.

THE MARCHI METHOD.—It was shown by Waller in 1852 that severed nerve fibers undergo degeneration (wallerian degeneration) distal to the level of section. It is now known that this is due to cutting off the distal part of the fiber from its trophic center, the cell body. The degeneration of the axis cylinder is accompanied or followed by degeneration of the myelin sheaths. The latter undergo chemical changes which make the fatty substances, after a proper interval, reduce osmic acid if the tissue has previously been fixed in potassium dichromate. The droplets of myelin of the degenerated fibers become blackened by the osmic acid, while the surrounding normal nervous tissue has a yellowish color. It therefore is easy to follow the course of degenerated fiber tracts in serial sections. The Marchi method has many pitfalls but is indis-

pensable in tracing the fiber tracts from the site of an experimental lesion.

METHOD OF EXTIRPATION.—Von Gudden devised the method of extirpating sensory organs, such as the eye, in very young animals, subsequently studying the brain for regions of developmental arrest. Much information as to location of sensory centers was obtained by this method, which supplements the method of comparative anatomy.

PHYSIOLOGIC METHODS

Physiologic methods have consisted fundamentally of studying the results of extirpation or of stimulation of parts of the nervous system in the living animal. The two methods have complemented each other. Strychnine serves as a nerve stimulant apparently through lowering synaptic resistance. This fact has been utilized, especially by Dusser de Bar  nne, in studying the activity of circumscribed nervous areas. Selective depressants, such as nicotine, applied to sympathetic ganglia, have also been used in greatly enriching the store of knowledge, not only of activity of different parts of the nervous system, but of location of many of the functional centers.

Pawlow developed the method of studying cortical activity by means of the conditioned reflex. In recent years this method has been combined with the methods of experimental lesions and the Nissl and Marchi degeneration methods for obtaining more exact information regarding the location of centers responsible for various functional activities. In the hands of Lashley, Allen and others this combination of methods is producing most valuable results.

A detailed account of the numerous methods employed would be very voluminous. Enough has been said to illustrate the types of technique employed and to give the student a slight basis on which to evaluate the results obtained.

NERVES AND GANGLIA

The brain and the spinal cord constitute the central nervous system. Nerves and ganglia, connected with the brain and cord, form the peripheral nervous system. The latter is in turn subdivided into cranial and spinal nerves and the so-called sympathetic system. The sympathetic system, however, is in part a component of both cranial and spinal nerves. The other components of those nerves terminate in end-organs, sensory or motor, which have to do with the relations of the body, primarily, to its external environment in capture of food, avoidance of danger, etc. These functions are usually referred to as *somatic* and the parts of the nervous system involved form the *somatic system*. The sympathetic system and related parts of the central apparatus are concerned with the processes of secretion, contraction of smooth muscle, digestion and excretion, the reproductive processes, etc. In general they have to do with visceral functions, and will be referred to as the *visceral system*.

The SPINAL NERVES in man number thirty-one pairs, including 8 cervical, 12 dorsal, 5 lumbar, 5 sacral, and 1 coccygeal. Each arises from the cord typically by two roots, a dorsal and a ventral, which unite to form a common nerve trunk (Fig. 30). The 1st cervical nerve emerges from the vertebral canal between the occipital bone and the atlas. The 8th cervical emerges between the 7th cervical and the 1st thoracic vertebrae. The 1st cervical nerve sometimes lacks the dorsal root, which typically is smaller in this nerve than the ventral root. The dorsal root of the spinal nerve has a swelling made of cells and fibers called the dorsal root ganglion (Figs. 30 and 31). The ventral root has no swelling and is made up entirely of fibers.

It was first suggested by Bell (1811) that the ventral roots are motor. Magendie (1822) demonstrated experimentally that the dorsal roots of spinal nerves are sensory and the ventral roots are motor. This important generalization is known as the law of Bell-Magendie or the law of the roots. The common nerve trunk resulting from union of the two roots contains both afferent and efferent fibers.

The DORSAL ROOT GANGLIA typically lie just outside the point where the dorsal roots penetrate the dura mater, and in the intervertebral foramina. The dorsal ganglia of the sacral nerves lie within the vertebral canal, and the ganglia of the 1st and 2nd cervical nerves lie on the arches of the atlas and the axis, respectively. The dorsal root ganglion is occasionally absent in the 1st cervical

nerve. The dorsal and ventral nerve roots penetrate the dura mater separately and each is covered peripherally by a continuation of this membrane. Where the roots join, the dural sheath becomes continuous with the epineurium of the common nerve trunk.

The ganglia are enlargements of ovoid form made up of nerve cells which give rise to the sensory fibers. Each cell has a single offshoot which branches in a T or Y manner into two processes, one of which passes centrally into the cord and the other passes peripherally into the nerve. The centripetal root fibers, on leaving the ganglion, collect into a bundle which breaks up into a series of rootlets. These enter the cord along the dorsolateral sulcus in a narrow longitudinal zone. The rootlets spread fanwise from the ganglion to the sulcus, in

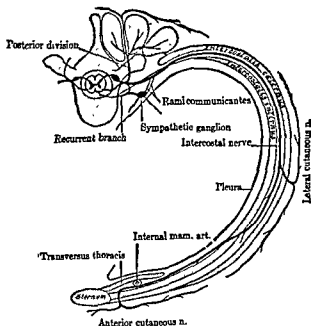


FIG 30—DIAGRAM OF TYPICAL SPINAL NERVE IN THORACIC REGION.

From Gray, *Anatomy of the Human Body*, Lea and Febiger

such a manner that the entire cord segment is included between the uppermost and lowermost twigs.

The ventral root fibers have their origin from multipolar cells in the ventral and intermediolateral gray columns of the cord. They emerge as a series of rootlets somewhat irregularly placed along the boundary zone between the lateral and the ventral funiculus. The emerging rootlets begin at the top and continue to the bottom of each cord segment. They also have a fanlike arrangement, the apex being formed by the rootlets converging distally to form the ventral root trunk.

THE COMMON NERVE TRUNK.—Dorsal and ventral roots unite just peripheral to the dorsal root ganglion to form the common nerve trunk, thus made up of mixed sensory and motor fibers. This mixed trunk is the spinal nerve and

emerges from the vertebral canal through the intervertebral foramen. Immediately after emerging it divides into *posterior* and *anterior primary divisions*. A short distance distal to the dividing point into these branches one or more *communicating branches* to the sympathetic chain ganglia are given off from the ventral division. A smaller *recurrent branch* to the meninges and blood vessels of the cord also arises from the common trunk, sometimes with twigs from the communicating branches.

The *posterior* or *dorsal primary division* supplies the back. The *anterior* or *ventral primary division* innervates the lateral and anterior parts of its respective

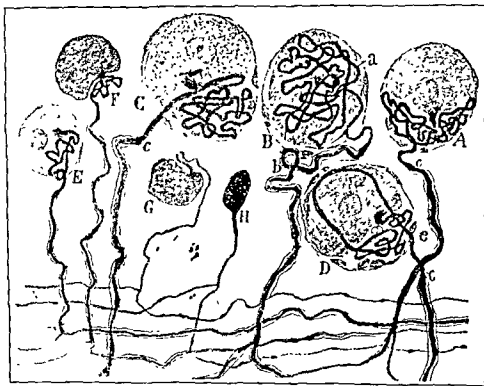


FIG. 31.—PORTION OF A SENSORY GANGLION. METHYLENE-BLUE.

A, cell with compact glomerulus; *B*, cell with diffuse glomerulus; *C*, large cell with polar glomerulus; *E*, cell whose axon forms an arc of a circle after it leaves the glomerulus; *E*, *F*, cells with simple glomeruli; *H*, cell without glomerulus; *c*, beginning of myelin sheath. From Cajal.

body segment. Each subdivides into branches which supply skin and muscles (Figs. 32 and 33). The cutaneous nerves are made up almost entirely of afferent fibers whose receptors lie in the skin. These receptors are of many types, described in Chapter 6. The muscular rami consist chiefly of motor fibers, terminating as motor end plates, on the muscle fibers. Intermingled with the motor fibers are numerous afferent fibers of muscle-sense. Both cutaneous and muscular nerves have, in addition, fibers to the blood vessels both of skin and muscles. The cutaneous bundles also convey pilomotor fibers and secretory fibers to the sweat glands.

The dorsal division of all the spinal nerves remain distinct, but the ventral

divisions are distinct only in most of the thoracic nerves. The cervical and upper thoracic ventral divisions branch and anastomose to form the cervical and brachial plexuses. In like manner the lumbar and sacral ventral divisions form the lumbosacral plexus. The brachial plexus supplies the upper extremity and the lumbosacral supplies the lower limb. Both extremities thus are innervated by the anterior divisions of the spinal nerves.

Section of a cutaneous nerve shows a histological picture of myelinated and unmyelinated fibers. The myelinated fibers are of large size, 15 to 20 microns in diameter. They terminate in various types of receptors such as pacinian corpuscles, Meissner's corpuscles, etc. Unmyelinated fibers are of two groups. Small fibers of one group pass to sweat glands and the smooth muscle of the *erectores pili*. These are derived from the sympathetic ganglia and must be

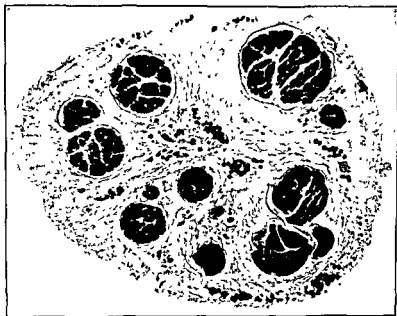


FIG. 32.—SECTION OF ULNAR NERVE, OSMIC ACID.

regarded as visceral motor fibers distributed to heat regulating mechanisms, etc., in the skin. The second group of unmyelinated fibers are of larger caliber and terminate as free nerve-endings which ramify in the stratified squamous epithelial layer of the skin. There are also nerve endings about the hair follicles which are stimulated by movements of the hairs, and which are connected with myelinated fibers. There are thus produced several types of afferent impulses, all belonging to the general cutaneous sense-organ which receives stimuli from the outside world. The impulses are conducted centrally by the myelinated fibers of the cutaneous nerves.

The *muscular nerves* consist also of myelinated and unmyelinated fibers. The latter are chiefly vasomotor fibers from the sympathetic chain ganglia. The former are chiefly motor fibers to motor end-plates, but intermingled as above

noted, and not to be distinguished histologically, are muscle-sense fibers which terminate in neuromuscular spindles.

The individual fibers from the various end-organs in the skin converge to form small nerve bundles. These in turn unite to form successively larger ones, and thus the cutaneous nerves, which are chiefly sensory, are built up. Entering into their structure also are the vasomotor, pilomotor and secretory fibers of the sweat glands, as already noted. The muscular nerves likewise are formed by aggregations of individual fibers to form small bundles, which in turn unite into

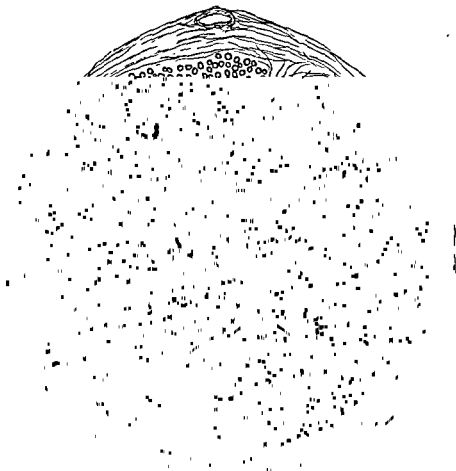


FIG. 33—A FUNICULUS OF A HUMAN ULNAR NERVE.

larger trunks. Cutaneous and muscular nerves unite to form the common nerve trunks.

White and Gray Communicating Rami.—In addition to the main division of spinal nerves into dorsal and ventral rami the nerves from the 1st thoracic to the 2nd to 4th lumbar body segments have branches which connect with the corresponding ganglia of the sympathetic trunk (Figs. 30 and 103). These are called the *white rami communicantes*. They are of glistening white color because made up of myelinated fibers. In addition to the white rami, the thoracic and upper lumbar spinal nerves have also one or more *gray rami communicantes*,

connecting them with the sympathetic chain ganglia. They are, in general, parallel with the white rami, lying close to them. The other spinal nerves have gray rami only, made up of unmyelinated fibers of Remak. They convey these fibers from the sympathetic chain ganglia, in which are located the nerve cells giving rise to the fibers to the spinal nerve trunk, to be distributed by it and its branches.

The *preganglionic fibers*, i.e., those passing through the white rami to the ganglia, have their origin from cells in the intermediolateral column of the spinal

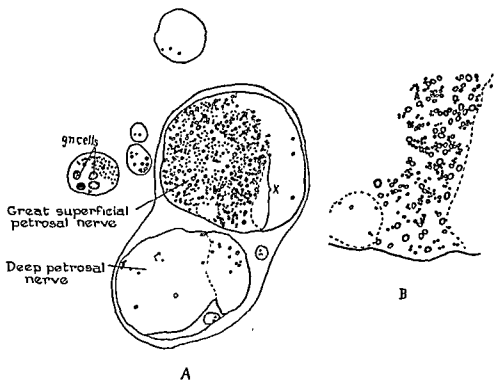


FIG. 34—CROSS-SECTION OF HUMAN VIDIAN NERVE, OSMIC ACID

A, section through entire nerve, showing large and small myelinated fibers and area of unmyelinated fibers (unstained) in the great superficial petrosal nerve, with only a few myelinated fibers, and large area of unstained unmyelinated fibers in the deep petrosal nerve. *B*, area designated by *X* in *A*, more highly magnified.

cord (Fig. 103). Their terminations are in the ganglia, either of the sympathetic trunk or of collateral ganglia, such as the celiac. Typically they are small, myelinated fibers, 1.5 to 4 microns in diameter. In the ganglia they make synaptic connections with the cells of the unmyelinated *postganglionic* fibers distributed as above described. Both, therefore, are visceral motor fibers, arranged in a chain of two links. The preganglionic neuron of the chain connects, through its terminal branches, with many postganglionic neurons. They thus diffuse the impulses they carry to many gland units or smooth muscle fibers.

Afferent Fibers.—In addition to the small myelinated preganglionic fibers,

white rami contain some myelinated fibers of large size (10 to 20 microns). These are not interrupted in the chain ganglia, but continue through them into the splanchnic and other visceral nerves attached to the sympathetic trunk (Fig. 103). These fibers in the viscera terminate in a number of types of receptors, stimulated by visceral processes of various kinds. On reaching the spinal nerves through the white ram these large myelinated fibers enter the dorsal roots, to reach the cord through them. Their cells are located in the dorsal root ganglia.

The spinal nerves therefore consist of several main functional types of fibers, which at least between the white rami and the junction of dorsal and ventral roots, are four in number, namely, *somatic afferent*, *visceral afferent*, *visceral*

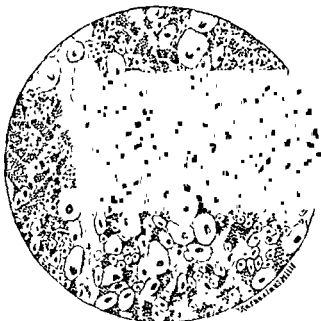


FIG. 35—CROSS-SECTION OF THE TRUNK OF THE HUMAN VAGUS NERVE, SOME DISTANCE BELOW THE NODOSE GANGLION, SHOWING MYELINATED AND UNMYELINATED FIBERS.

Pyridine silver X680. From Jordan, *A Textbook of Histology*, 7th ed, D. Appleton-Century Co., Inc., New York, 1937. (After Ranson.)

afferent and *somatic efferent*. The somatic afferents serve cutaneous sense. The somatic efferents supply the voluntary muscles, which, in general, relate the position of the body with reference to its environment. The visceral efferents supply smooth muscle and glands, wherever located, and visceral afferents convey to the cord stimuli from visceral receptors which produce visceral reflexes.

The Dermatome.—Each pair of spinal nerves supplies a segment of the body, in keeping with the fundamental metameric pattern. The anterior roots primarily supply efferent fibers to the segmental musculature. Their branches may be carried far from their segment of origin by migration of muscles during embryonic development, but the roots retain their segmental pattern. The anterior roots in addition contain efferent fibers which reach the blood vessels of the

skin, serving a vasoconstrictor function. They also contain fibers to the sweat glands and the erector muscles of the hairs. The posterior roots carry sensory fibers primarily, but there are indications of vasodilator fibers also. The evidence concerning the latter is conflicting and there is no accord on the question at present. The area of skin supplied by the spinal roots of a given nerve is known as a *dermatome*. Most of the dermatomes overlap so that sensation is not entirely lost in the skin after section of the sensory root of a given body segment. Section of adjacent nerves on both sides is necessary to completely destroy sensation or to abolish vasomotor effects in the skin. The area of distribution of

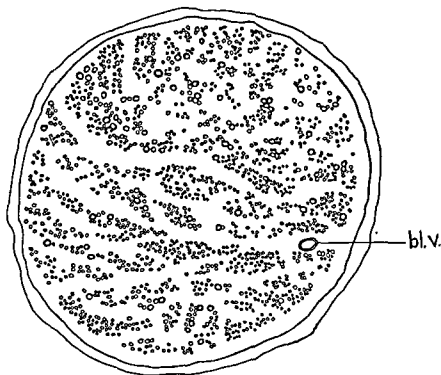


FIG. 36.—SECTION OF VAGUS NERVE OF RABBIT, SHOWING MYELINATED FIBERS OF VARIOUS SIZES, AND SPACES BETWEEN LARGELY OCCUPIED BY UNSTAINED UNMYELINATED FIBERS *bl.v.*, BLOOD VESSEL. OSMIC ACID.

tactile fibers from a given nerve is greater than that supplied by pain and temperature fibers.

Functional Types of Fibers.—From study of the electric currents found in nerve fibers during conduction of stimuli (action currents) it has been found that different rates of oscillation are conveyed by fibers of distinct histological types. Mixed nerves show three groups of waves, which have been designated the A, B and C groups. The A waves have a wide range of conduction rate, up to about 100 meters per second. They are carried by the larger myelinated fibers of the somatic motor and part of the somatic sensory categories. The somatic motor impulses show the most rapid oscillographic vibrations. The afferent

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impulses producing waves in the A group include touch, pressure and proprioceptive sense. The B waves are carried by the small myelinated fibers. The oscillations in this group are less rapid and are produced by stimuli of pain which can be localized and of temperature. The C group of oscillations are the slowest, falling below 1.7 meters per second. They are conducted by the unmyelinated fibers and represent stimuli of pain which cannot be localized and vasomotor impulses.

CLINICAL INTERPRETATION

SOME LESIONS OF THE SPINAL NERVES

Section of posterior nerve roots distal to the ganglia, or injury to them or their ganglia, results in segmental disturbances of pain, temperature, touch, pressure, muscle sense and visceral sensibility; loss of superficial and deep reflexes; loss of muscle tone; incoordination of muscular movements, and trophic changes. Due to overlapping of nerves from adjacent segments the skin anesthesia is complete only when one or more additional nerves are sectioned on each side of the segment primarily involved. Loss of muscle tone and muscular incoordination are due to interruption of the proprioceptive pathway to the spinal cord and brain. The trophic changes, especially in the skin, are due to loss of some trophic influence which peripheral nerve fibers exercise on the area of skin they innervate.

A good example of the sensory and trophic disturbances which have a strictly dermatomal distribution, and which result from injury to individual dorsal roots and their ganglia, is to be found in the effects of herpes zoster. This disease is regarded as due to a virus which attacks the posterior roots and their ganglia. One or more posterior roots may become involved. The symptoms, namely, redness of the skin, followed by burning, sticking sensations and severe pains in the skin, with formation of blisters along the course of the nerve involved, are accounted for by irritation of the sensory fibers of the posterior roots and their ganglion cells by the virus. The sensory disturbances are regarded as due to stimulation of sensory fibers, while the blisters are due to trophic factors.

Section of anterior roots of spinal nerves, or destruction of their nerve cells in the anterior gray column (lower motor neurons), results in flaccid motor paralysis of the muscles supplied. In this type of paralysis there is loss of segmental reflexes, loss of muscle tone, gradual wasting of the muscles innervated by the injured neurons, and appearance of the reaction of degeneration. This reaction is failure of the muscle to respond to the faradic current, an induced alternating electric current, but response by slow, worm-like contractions to the galvanic current, which is a direct current from a chemical battery. This galvanic response also disappears with further degeneration. If the preganglionic neurons of the thoracolumbar autonomic system are involved, mottling of the skin and reduced surface temperature may also appear, indicating vasomotor paralysis. In infantile paralysis (anterior poliomyelitis) the anterior column cells are be-

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lieved to be affected by a virus which causes them and their fibers to degenerate. The cells affected may be localized or the infection may involve the neurons supplying many muscles.

Section of the common nerve trunk just distal to the junction of posterior and anterior roots results in complete loss of all types of sensations (somatic and visceral afferent) and in motor paralysis (somatic efferent) of the flaccid type. Both sensory and motor fibers show wallerian degeneration distal to the injury since both types of fibers are cut off from their cell bodies in the posterior root ganglia and the anterior gray columns of the spinal cord, respectively. If the thoracic or upper lumbar nerves are involved vasomotor phenomena result from injury to visceral efferent vasoconstrictor fibers in these nerves.

Section of the posterior root of a spinal nerve between the ganglion and the spinal cord results in loss of all sensation and reflexes. Centripetal degeneration of the posterior root fibers takes place, since they are cut off from their cells of origin in the ganglion. Unless the ganglion cells are damaged centrifugal degeneration does not occur when the central processes are cut or injured. Degeneration of small myelinated fibers in the posterior roots distal to the ganglion has been described following section between ganglia and spinal cord. Such fibers have been interpreted as vasodilators having their origin with the spinal cord and emerging through the posterior roots. The evidence is confusing and there is little agreement regarding such fibers.

Section of a purely sensory peripheral branch of a spinal nerve, such as the lateral femoral cutaneous nerve, results in loss of all sensation in the skin area supplied, which in the case of the nerve mentioned is the lateral part of the thigh. Irritation of such a nerve results in tingling, stabbing and burning pains in the region supplied, as in *meralgia paraesthetica* when the lateral femoral cutaneous nerve is involved.

Section of a mixed motor and sensory branch such as the circumflex axillary nerve, which is an isolated peripheral nerve, results in flaccid motor paralysis of the muscles supplied and in the loss of all cutaneous sensation in the skin area innervated. In the case cited the deltoid muscle and the teres minor would lose voluntary motility and show wasting and the reaction of degeneration because the lower motor neuron is involved. Cutaneous sensation would be entirely lost in the upper lateral part of the upper arm, with only partial loss in an area bordering on the zone of complete anesthesia. The partial retention of sensation in this zone would be due to overlap by sensory fibers from adjacent body segments.

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CHAPTER 6

RECEPTORS AND EFFECTORS

RECEPTORS

A receptor may be defined, in Sherrington's phrase, as a structure designed to lower the threshold of excitability for one type of stimulus and to heighten it for all others. Receptors may be classified into three main groups, namely, *exteroceptors*, *proprioceptors*, and *interoceptors*. Exteroceptors receive stimuli from the outside world and thus supply the body with information concerning

A

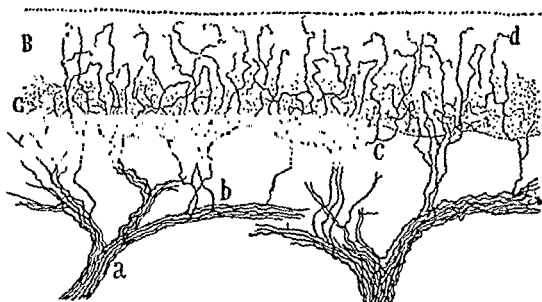


FIG. 37.—FREE NERVE ENDINGS IN EPITHELIUM.

A, stratum corneum; B, malpighian layer; C, pigmented zone; a, nerve fiber bundle; b, c, bifurcations of nerve fibers; d, terminal branches in the epithelium. From Cajal, *Histology*, Wm. Wood & Co., Baltimore, 1933.

its environment. Since such information is of importance to the body as a whole these receptors and the nervous mechanisms related to them are grouped together under the term *somatic afferent* or *sensory system*.

PROPRIOCEPTORS are stimulated by activity of muscles, movements of joints, etc. The sensations may or may not reach consciousness. In carrying out the muscular activities necessary to bodily adjustment to environment, capture of

food, etc., the proprioceptors play an important role in bringing about proper coordination of muscles. They are therefore related functionally to the exteroceptors, although they receive their stimuli from nerve-muscle spindles and other nerve endings located within the muscles and other organs of the body, rather than in the skin or on the body surface, as is true of the exteroceptors. The proprioceptors will be considered as a separate group serving muscle sense and related sensations.

The **INTEROCEPTORS** primarily serve the visceral organs of digestion, respiration, reproduction, etc. The impulses do not, as a rule, reach the conscious level, but serve to initiate reflexes concerned with visceral processes. With their nerve fibers and central connections they are included under the *visceral afferent* system.

Changes in the environment of the receptor or *stimuli*, if strong enough, excite the end-organs to give rise to nerve impulses in the nerve fiber connected with them. The fibers convey the impulses to the brain or spinal cord. If the stimulus is too weak, no impulse results. The receptors may be thought of as triggers which initiate impulses under conditions appropriate to the respective organs, giving rise to specific sensations.

EXTEROCEPTORS are of many types. They include such special sense organs as the eye, the organ of hearing and others which will be considered in relation to the systems they serve. The skin also may be regarded as a general sensory organ, in addition to its protective function. It contains many types of sensory nerve endings belonging to the general somatic sensory group. Some of these will be described.

The simplest type of receptor, from the viewpoint of histological structure, is repre-



FIG. 38—TACTILE CELLS IN THE EPITHELIUM OF THE GROIN OF A GUINEA-PIG

a, tactile cell, e, epithelial cell; m, tactile meniscus, at the end of a nerve fibril; n, nerve fiber. Chloride of gold. Highly magnified. (After Ranvier)



FIG. 39—NERVE ENDINGS IN HAIR FOLLICLE OF DOG

Gold chloride preparation (From Barker after Bonnet)

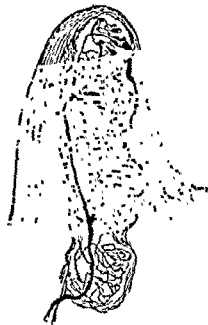


FIG. 40.—TACTILE CORPUSCLE OF MEISSNER.

Nerve fibrils which enter the corpuscle and supply its nerve skein. Methylene blue. Very highly magnified. (After Dogiel.)

Any stimulus tending to injure the cell could therefore be interpreted as producing pain.

In Woollard's investigations, on human subjects, he obtained evidence that pain, cold and touch have specific endings. Definite points in the dermis and epidermis gave rise to specific sensations. So long as a fragment of the specific ending was present, the specific receptor quality persisted, but disappeared when the ending was cut away.

Tactile sensibility is served by several types of endings. The simplest in histological pattern, next to free nerve endings above described, are Merkel's tactile discs (Fig. 38). These consist of expanded discs on the terminal twigs of nerve fibers which branch in the stratified squamous epithelium. Each terminal disc is attached to a modified epithelial cell. Such endings are held to be excited by tactile stimuli on the surface of the

sented by the free nerve endings in the epithelium. These are terminal branches ending among the cells of the stratified squamous epithelium. Similar free nerve endings are found in the cornea, in the tympanum and in the teeth, locations whence pain sensations only are recognizable. It is usually held therefore that such free nerve terminations are pain receptors. Waterston found no evidence of pain stimulation in the human skin until the corium was reached. He interpreted the free endings in the epidermis as giving rise to sensations of touch.

Woollard has recently described networks of unmyelinated fibers and also free nerve endings in the deep layers of the skin, in blood vessels and in some of the viscera. These are terminations of unmyelinated and small myelinated fibers, the latter giving rise to free endings in the epidermis which appear to be receptors for localized pain. There is evidence that some types of nerve fibers end within epithelial cells.

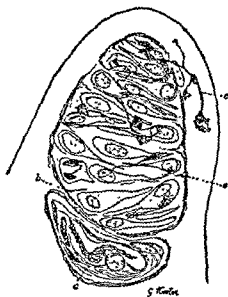


FIG. 41.—TACTILE CORPUSCLES OF MEISSNER.

b, epithelioid cells; *c*, nerve endings; *e*, connective tissue capsule. (Maximow, after Van de Velde.)

RECEPTORS AND EFFECTORS

skin above them. Many of the hair follicles are surrounded by special skeins of nerve fibers (Fig. 39), with several types of endings, which are stimulated by touch at the base of the hairs and by movements of the hairs themselves. It has been shown experimentally that the endings about hair follicles are tactile receptors, and it is well known that shaving a surface of the body reduces its sensitivity to touch.

Meissner's tactile corpuscles (Figs. 40 and 41) are found in the connective tissue papillae of the skin, especially of the parts of the body particularly sensitive to touch. They are elliptical or somewhat cylindrical structures made up of a many layered capsule of connective tissue, with thin connective tissue plates dividing the corpuscle into narrow transverse spaces. These plates have nuclei transversely placed with reference to the major axis of the corpuscle. Large myelinated nerve fibers, one or more, reach the corpuscle, where they lose the myelin sheath. The naked axis cylinder branches within the capsule into the spaces between the transverse strands. In addition to the large main nerve fibers there are one to four fine axis cylinders with numerous varicosities which also enter the capsule and remain distinct from the branches of the main fibers. Meissner's corpuscles are 40 to 100 microns in length and 30 to 60 microns in diameter. They are found in the skin of all parts of the body, and are numerous in the hand, foot, nipple, lip and tip of tongue.

Pacinian corpuscles, also called after Vater (Fig. 42) are found in various parts of the body, such as the subcutaneous tissue of the fingers and near joints, in the mesentery, and in the connective tissue of various organs, as the pancreas. They are white oval bodies formed of a capsule which consists of many concentric, thin layers of connective tissue enclosing an inner bulb or cylindrical space, into which enters a large, myelinated nerve fiber. The neurolemma and sheath of Henle of the nerve fiber becomes

continuous with the capsule of the corpuscle and the myelin sheath disappears at the base of the corpuscle. The naked axis cylinder passes through the inner bulb to the opposite end of the corpuscle. Here it ends in a thickening which frequently gives off small branches. Small blood vessels enter the base of the pacinian corpuscle and loops of capillaries ascend a little way between the lamellae of the capsule. Experimental evidence indicates that at least some of

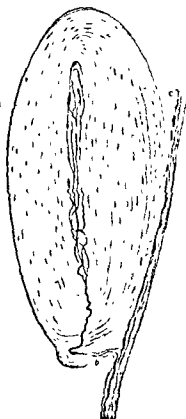


FIG. 42—A LAMELLAR CORPUSCLE FROM THE PLEURA OF A CHILD.

a, lamellae; b, nerve fiber; c, nerve. Methylene blue. Moderately magnified (After Dogiel) From Jordan, *A Textbook of Histology*, 7th ed., D. Appleton-Century Co., Inc., New York, 1937.



FIG. 43—END-BULB OF KRAUSE FROM THE MARGIN OF THE OCULAR CONJUNCTIVA.

The axon forms a dense skein within the encapsulated bulb. Methylene blue. Highly magnified. (After Dogiel) From Jordan, *A Textbook of Histology*, 7th ed, D Appleton-Century Co, Inc, New York, 1937.

this type are present in the connective tissue of muscles and tendons and in the mucosa of the mouth.

the corpuscles of Pacini have to do with regulation of blood pressure. They are regarded as the organs of deep pressure and possibly of vibration sensibility. Pacinian corpuscles are readily visible to the naked eye, having a length of 0.5 to 4.5 mm. and a diameter of 1 to 2 mm.

Krause's end-bulbs (Fig. 43) are encapsulated endings occurring in connective tissue. They have a diameter of 20 to 100 microns. They are found in the conjunctiva, the skin of the lips, the glans penis, etc. They are regarded as cold receptors, appearing to correspond to the cold spots of the skin.

Genital corpuscles (Fig. 44), found beneath the epithelium of the penis, clitoris and neighboring structures, are round or oval bodies 60 to 400 microns long. They receive numerous nerve fibers which branch to adjoining corpuscles and also to the epidermis.

Cylindrical end-bulbs of Krause have a central nerve fiber in an inner bulb containing a semifluid substance. Surrounding the inner bulb there are a number of layers of connective tissue. Bulbs of



FIG. 44—GENITAL CORPUSCLES FROM THE CLITORIS OF A RABBIT.

A single axon from the nerve plexus enters each corpuscle. Methylene blue. Highly magnified. (After Retzius) From Jordan, *A Textbook of Histology*, 7th ed, D Appleton-Century Co, Inc, New York, 1937

Corpuscles of Ruffini (Fig. 45) are found in the subcutaneous connective tissue of the fingers and elsewhere. They consist of elongated connective tissue bundles within which ramify axis cylinders of nerve fibers, ending in flattened expansions.

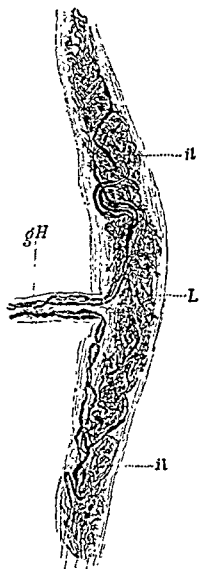


FIG 45—RUFFINI'S END-ORGAN

A single nerve fiber breaks up to form the tangle of nerve fibrils within the organ. *gH*, myelin sheath, *il*, terminal fibrils of the axis cylinder; *L*, connective tissue capsule. (After Ruffini) From Jordan, *A Textbook of Histology*, 7th ed, D. Appleton-Century Co, Inc, New York, 1937.

Corpuscles of Golgi-Mazzoni (Fig. 46) are found in tendons near the attachments of the muscle fibers. Nerve fibers, after losing their myelin sheaths, penetrate between fascicles of tendon fibers and ramify into terminal processes with many varicosities. The entire corpuscle is enclosed by a fibrous capsule con-

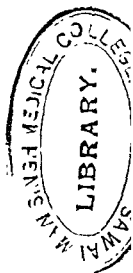




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ordinary striated fibers. The parent fibers enter the spindle at one pole and divide, the branches anastomosing and branching like heart muscle. Along the course of each muscle fiber occur bubble-like structures, 5 to 15 microns in diameter, more numerous near the center of the spindle. Two or more large myelinated nerve fibers enter the spindle, and several unmyelinated fibers also enter it. The sheath of Henle of the myelinated fibers becomes continuous with the capsule of the spindle. The fibers divide within the capsule into secondary and sometimes tertiary rami. These lose their myelin sheaths and break up into numerous branches with club-shaped or leaf-like endings which rest on those parts of the muscle fibers containing the translucent bubble masses. Other nerve fibers, after losing their myelin sheaths, wind about the muscle fibers as spiral bands, to terminate in expansions or to give off terminal branches in their course. The spiral endings may terminate on the striated part of the intrafusal muscle fibers. It has been claimed that there are two distinct types of endings



FIG 47.—A MUSCLE SPINDLE FROM THE PSOAS MAGNUS OF MAN.

1, intrafusal muscle fibers; 2, nerve fibers; 3, axial sheath; 4, connective tissue capsule; 5, muscle fibers of an adjacent fasciculus; 6, periaxial lymphatic spaces; 7, blood vessel. Hematein and eosin X470. From Jordan, *A Textbook of Histology*, 7th ed, D. Appleton-Century Co, Inc, New York, 1937.

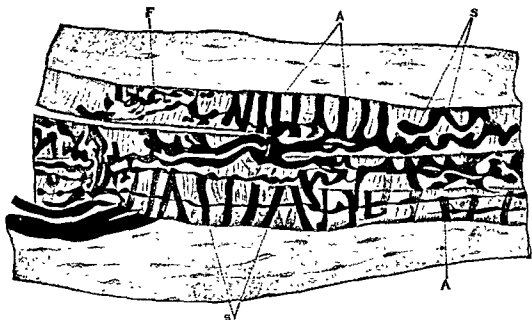


FIG 48—MIDDLE THIRD OF A TERMINAL PLAQUE IN THE MUSCLE SPINDLE OF AN ADULT CAT.

A, rings, F, dendritic branchings, S, spirals Chloride of gold preparation Highly magnified (After Ruffini) From Jordan, *A Textbook of Histology*, 7th ed, D. Appleton-Century Co, Inc, New York, 1937.

tinuous with the covering of the tendon. A lymph space is found between the corpuscle and the capsule.

Neuromuscular spindles (Figs. 47 and 48) consist of bundles of small muscle fibers, 3 to 10 in number, surrounded by a capsule of many layers of connective



FIG. 46.—GOLGI-MAZZONI CORPUSCLES FROM THE SURCUTANEOUS TISSUE OF THE TIP OF THE FINGER. (After Ruffini.)

From Jordan, *A Textbook of Histology*, D. Appleton-Century Co, Inc, New York, 1937.

tissue. Nerve fibers penetrate the capsule and ramify on the muscle fibers. The organ as a whole is spindle-shaped, although compound organs of this type may have a number of dilatations. Each spindle has an independent lymph and blood supply. There is a space between the external capsule and an internal capsule around the muscle fibers which is filled with lymph.

The muscle fibers are striated but have only about one-third the diameter of

in the spindles, supplied by distinct nerve fibers, but this view has not generally been accepted. The unmyelinated fibers which enter the spindles are regarded as vasomotor, in part. Other fine fibers have club-like endings whose function is not known. The length of neuromuscular spindles is usually stated as 2 to 4

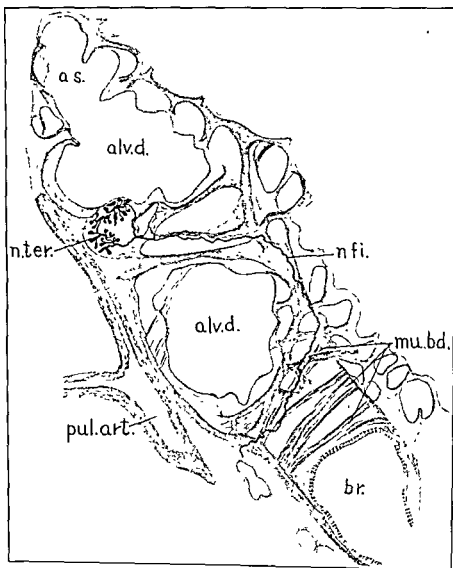


FIG. 51—NERVE ENDING IN WALL OF ALVEOLAR DUCT.

alv.d., alveolar duct; *a.s.*, air sac; *br.*, bronchiole; *mu.bd.*, muscle band; *n.fi.*, nerve fiber; *n.ter.*, nerve termination. From *Am. J. Anat.*, 1933, 52: 137.

mm. in man, with a diameter of 0.04 to 0.4 mm. There is, however, a variation from 0.05 mm. to 13 mm. in length.

Neurotendinous organs (Fig. 49) are found characteristically at the junctions of muscles and tendons and in the aponeuroses related to muscles. There is some variation as to their position. In the muscles they are found in the muscular sheaths rather than in the tendons. Sometimes they lie completely in the tendon. Each spindle has an independent blood supply. It consists typically of a number

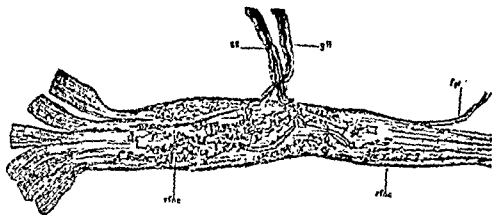


FIG. 49—NEUROTENDINOUS END-ORGAN OR TENDON SPINDLE OF GOLGI.

tft, bundle of tendon fibers; *gII*, myelinated nerve fiber; *rtae*, ribbon-like terminal ramifications of the axon; *SR*, node of Ranvier. Moderately magnified. (After Ciaccio) From Jordan, *A Textbook of Histology*, D. Appleton-Century Co., Inc., New York, 1937.

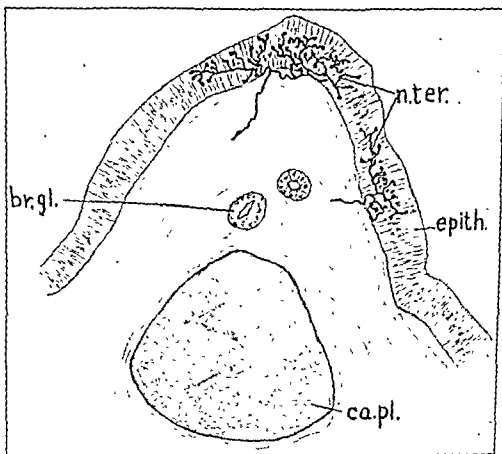


FIG. 50—NERVE ENDING IN BRONCHIAL EPITHELIUM.

br.gl., bronchial gland; *ca.pl.*, cartilage plate; *epith.*, epithelium; *n.ter.*, nerve termination. From *Am. J. Anat.*, 1933, 52: 137

RECEPTORS AND EFFECTORS

many thousands of such fibers form the olfactory filae and extend through the cribriform plate to enter the olfactory bulb of the brain. The free ends of the neuro-epithelial cells are covered with from 8 to 10 cilia. Between the olfactory cells lie tall columnar epithelial supporting cells. The olfactory cells are chemical receptors which test substances inhaled with the air and thus pass over the olfactory membrane. Minute particles of such substances come into contact with the cilia and in some manner set up stimuli within the cells which are transformed into nerve impulses to the olfactory bulb.

The *gustatory sense organs* occur in the form of spindle-shaped groups of cells in the stratified squamous epithelium of the tongue in the adult, and also

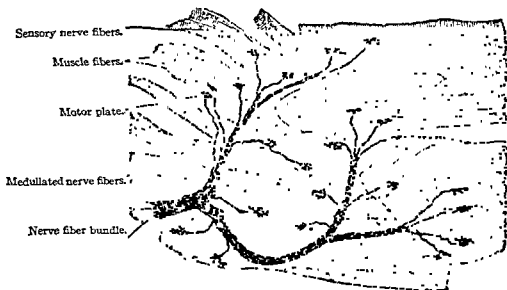


FIG. 53—MOTOR END-PLATES ON STRIATED MUSCLE FIBERS.

From J. L. Bremer, P. Blakiston's Son & Co, Philadelphia, 1936.

in the pharynx in infants. Two kinds of cells make up the taste bud, which is an elliptical body with a *pore* opening to the surface. The *neuro-epithelial cells* have cilia at the free end which project through the pore. The more rounded basal end is surrounded by a terminal tuft of nerve fibers from the gustatory nerves. The other type is called the *sustentacular cell*. These cells apparently form a supporting framework for the neuro-epithelial cells. The latter transform appropriate chemical stimuli into the four primary sensations of taste, namely, sweet, sour, salty and bitter. Various flavors, aside from these, are produced by combinations of gustatory and olfactory stimuli.

EFFECTORS

The *effectors* of the somatic efferent system are usually considered of but one type, namely, the *motor end plate* on striated muscle fibers. The muscular nerves, composed chiefly of myelinated nerve fibers, break up into bundles which

of tendon fascicles with numerous nuclei, enclosed within a capsule of connective tissue. A large myelinated nerve fiber, or sometimes two or three such fibers, enter the spindle, usually at the center. On reaching the spindle the sheath of Henle becomes continuous with the capsule. The fibers retain their myelin sheaths and break up into primary, secondary and tertiary branches. The latter subdivide into branches without myelin, which pass between and around the tendon bundles, giving off smaller branches with leaf-like plates which form a network around the primary bundles. Neurotendinous spindles have a length of 1.28 to 1.42 mm. and a breadth of 0.17 to 0.25 mm. in man, according to Koeliker.

VISCERAL AFFERENT RECEPTORS OR INTEROCEPTORS are found in mucous membranes of various viscera, in the muscular layers of viscera, etc. They are of relatively simple pattern as compared with the exteroceptors and proprioceptors above described.

In the epithelium of the trachea and larger bronchi nerve endings are present (Fig. 50) which have short twigs terminating in varicosities, apparently between the epithelial cells. They respond to mechanical stimuli. Endings of different type are found near the extremities (Fig. 51) of the air passages and suggest chemoreceptors. The intestine has nerve terminals between the epithelial cells which are regarded as afferent receptors. In the wall of the urinary bladder Retzius has described nerve endings of afferent type.

In the aorta and the carotid body, chemoreceptors are present, according to

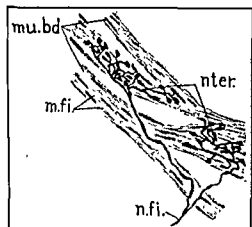


FIG. 52.—SMOOTH MUSCLE NERVE SPINDLES.

mu.bd., muscle band; *m.fi.*, muscle fibers; *n.fi.*, nerve fibers; *ntr.*, smooth muscle nerve spindles. From *Am. J. Anat.*, 1933, 52 141.

physiological and histological evidence. In the muscular coat of the stomach Carpenter described peculiar endings between the muscle bands which probably are stimulated by activity of the muscle layer. "Smooth muscle nerve spindles" have been described in the bronchial muscle bands (Fig. 52) of animals and man. Kleyntjens and Langworthy have described somewhat similar endings in the muscular layer of the urinary bladder. These various types of visceral receptors, widely distributed in the visceral organs, may be termed *general visceral afferent* receptors. The *special visceral afferent* system has as end organs such special sensory organs as taste buds and olfactory cells.

Olfactory sensory cells are the most primitive, structurally, of all the receptors in man. They consist of neuro-epithelial cells in the olfactory membrane which are prolonged at the basal end into varicosed unmyelinated nerve fibers. The

RECEPTORS AND EFFECTORS

Terminations en Grappes.—Some axons leading to striated muscle end in small loops or bulbar enlargements, either below or outside the sarcolemma. These are regarded by Hines as simple motor endings.

General Visceral Efferent Terminations.—Fine nerve fibers from cells in ganglia of the autonomic system end in relation to smooth muscle fibers or on the secretory epithelium of glands in various parts of the body. The terminals for smooth muscle fibers are in the form of minute knobs located near the

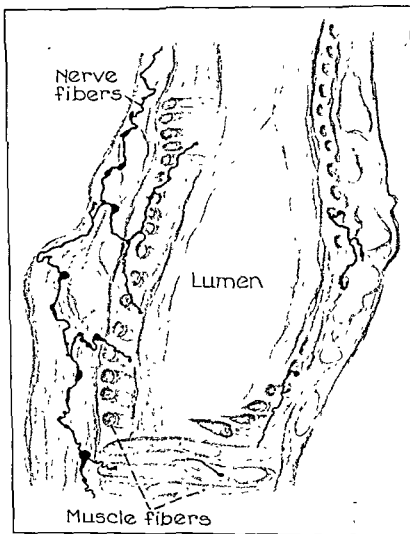


FIG. 56.—NERVE ENDINGS ON MUSCLE FIBERS IN ARTERIOLE.

nucleus (Fig. 56). Huber and DeWitt described such knobs on the surface of the muscle fibers (Fig. 55). Intracellular knobs have also been described, suggesting the possibility of two forms of stimulation. The terminals on secretory epithelium are in the form of fibers in contact with the cells, or ending within the cells, according to some investigators.

The motor endings in heart muscle are somewhat larger than in smooth muscle

run in the intermuscular septa. From these, still smaller bundles pass into the muscle fascicles to fray out into individual fibers which end in the form of motor plates, usually near the middle of the individual striated muscle fibers. Each muscle fiber is believed to receive one or sometimes two branches. The neuro-

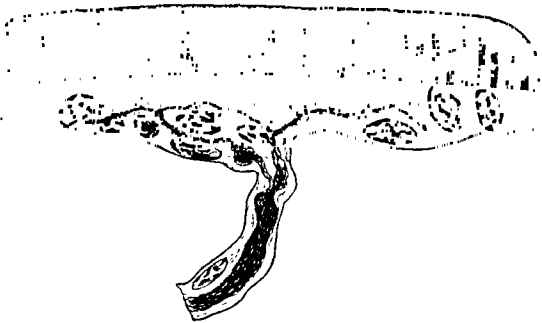


FIG. 54—MOTOR END PLATE.

Bremer, *Textbook of Histology*, P. Blakiston's Son & Co., Philadelphia, 1936. After Boeke.

lemma of the nerve fiber is usually described as continuous with the sarcolemma of the muscle fiber. The myelin sheath ends on reaching the sarcolemma, and the nerve fiber branches out into an area of modified granular sarcoplasm which forms an elevated area 40 to 60 microns in diameter on the muscle fiber. This

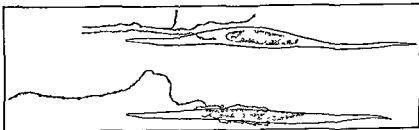


FIG. 55—SMOOTH MUSCLE MOTOR ENDINGS.

Redrawn from Huber and DeWitt.

elevated area is characterized by numerous nuclei in the sheath, regarded as derived from neurolemma and sarcolemma jointly. The nerve fibers break into fibrils, which form a periterminal net. Each nerve fiber divides into numerous terminal fibers, each supplying a motor plate (Figs. 53 and 54).

CHAPTER 7

THE SPINAL CORD AND MENINGES

In man the spinal cord (Fig. 57) occupies the upper two-thirds of the neural canal of the vertebral column. It extends from the margin of the foramen magnum to the lower border of the 1st lumbar vertebra or the upper border of the 2nd lumbar vertebra. In the male the average length of the cord is 45 cm., in the female 43 cm. During the first three months of embryonic development the spinal cord extends to the lower end of the neural or spinal canal. In subsequent growth of the body, however, the vertebral column lengthens more rapidly than does the cord. At birth, as a rule, the cord ends opposite the 3rd lumbar vertebra. During childhood the spinal column continues to increase in length at a faster rate than does the cord, resulting in the adult relations described.

The spinal cord is continuous above with the medulla oblongata. The level at which the cord begins is defined as that corresponding with the uppermost rootlet of the 1st cervical nerve, which is at the foramen magnum. The lower end tapers to a point, the conical extremity being known as the *conus medullaris*. A thread-like extension from the conus, known as the *filum terminale* (Fig. 58) continues downward in the spinal canal and is attached to the back of the coccyx. The filum is composed of pia mater containing a prolongation of the central canal of the cord in its upper portion. It also contains a few rudimentary nerve fibers. The lower portion of the filum is joined by a continuation of the dura mater which forms a *filum terminale externum*.

The lower third of the spinal canal contains, in addition to the filum terminale, bundles of nerve fibers. These, in general, run parallel with the long axis of the cord. They are the trunks of the lumbar, sacral and coccygeal spinal nerves, which were laid down as segmental nerves in the early embryo and became attached in the intervertebral foramina when the vertebrae were formed. When the vertebral columns began to elongate at a more rapid rate than the cord, these nerves were drawn downward within the spinal canal. This mass of nerve fibers is called the *cauda equina*. Most of the other spinal nerves also extend from the cord to their respective foramina at various angles other than the right angle of early embryonic development, because of the same factor of unequal growth of spine and cord.

THE MENINGES

DURA MATER.—The spinal cord is surrounded by three membranes, collectively called the *meninges*. The outermost is the dura mater. This is a tubular sheath

and frequently have a small cluster of terminal knobs. Otherwise they appear quite similar to those of smooth muscle.

Special Visceral Efferent Terminations.—These are motor end-plates histologically identical with those on striated muscle generally. The muscles derived from the branchiomeres, i.e., the muscles of mastication and the hyoid apparatus, as well as the pharyngeal muscles, are regarded as a special group of visceral muscles. They retain their branchial nerve supply, but both nerve fibers and motor endings are modified into the types characteristic, histologically, for somatic muscle.

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THE SPINAL CORD AND MENINGES

From the inner surfaces of the lateral walls of the spinal dura are given off the *denticulate ligaments* which suspend the cord in the dural tube. These ligaments are attached at intervals to the dura by 20 to 22 denticulations between the spinal nerves. They spread out fan-wise, medially, to form a nearly continuous line of attachment to the pia mater between the anterior and posterior nerve roots.

The ARACHNOID (Fig. 59) is the middle coat of the meninges. It is a thin, continuous sheet of connective tissue separated from the dura mater by a thin

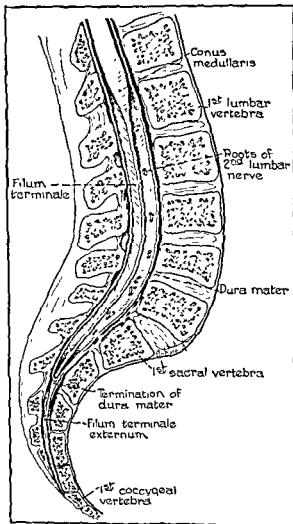


FIG. 58.—FILUM TERMINALE AND LOWER PART OF SPINAL CORD.

subdural space. It is attached to the pia mater by fine bundles of arachnoidal tissue which traverse the considerable *subarachnoid space*. The latter is filled with cerebrospinal fluid. At the lower end of the spinal canal it forms a *spinal arachnoid sac* which contains the lower end of the cord and the cauda equina.

The PIA MATER (Fig. 59) is a delicate layer of connective tissue which closely invests the surface of the cord. Anteriorly it folds into the anterior median

of dense fibrous tissue which continues from the foramen magnum to the level of the 2nd or 3rd sacral vertebra (Figs. 58 and 59). Its upper end is attached to the margin of the foramen magnum and to the 2nd and 3rd cervical vertebrae. At its lower end it is attached through its continuation as the *filum terminale externum*, above mentioned, to the periosteum of the back of the coccyx.

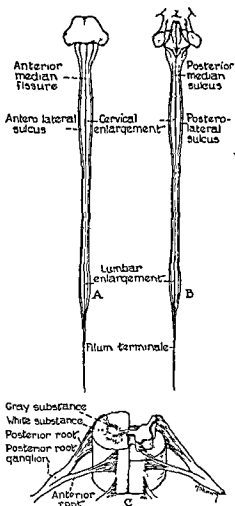


FIG 57.—DIAGRAMS OF SPINAL CORD

anterior view B, posterior view C, a segment of the spinal cord with anterior and posterior nerve roots attached

Lateral prolongations, in the form of tubular sheaths of dura, accompany the spinal nerves into the intervertebral foramina. Anteriorly, loose fibrous attachments connect the dura with the posterior longitudinal ligament of the vertebral column. Posteriorly there are no attachments to the wall of the neural canal. Between the outer surface of the spinal dura and the periosteum of the vertebrae, which corresponds to the outer layer of the cranial dura, there is an *epidural space* containing fat and veins with thin walls.

THE SPINAL CORD AND MENINGES

to the walls of the spinal canal. The cord is thus suspended in a tube of fluid.

The anterior surface of the cord is deeply grooved in the midplane by a cleft, the *anterior median fissure*, throughout its length. This contains a fold of pia mater and blood vessels. It extends inward about one-third of the anteroposterior diameter of the cord. The *posterior median septum* is a narrow partition made up of ependymal tissue and neuroglia between the two halves of the cord dorsally. In the cervical and thoracic parts of the cord the dorsal septum extends deep, but is shallower in the lumbar cord. On each side there is a *posterolateral sulcus* along which the dorsal root fibers enter the cord. This sulcus marks the boundary, externally, between the dorsal and the lateral funiculi. It extends the entire length of the cord. In the cervical region there is a *posterior intermediate*

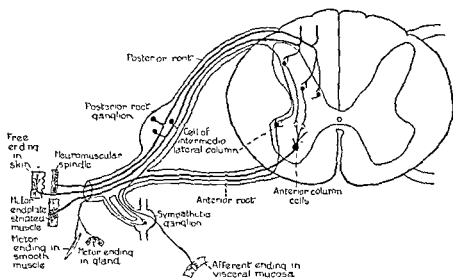


FIG. 60.—DIAGRAM OF SPINAL CORD AND SPINAL NERVE ROOTS.

sulcus, formed by a septum of pia mater which penetrates superficially between the fasciculus gracilis and the fasciculus cuneatus. It continues into the medulla oblongata between the nuclei of these fiber bundles. Anteriorly a somewhat arbitrary line, corresponding to the lateralmost filae of the ventral nerve roots, divides the ventral from the lateral funiculus. The filae of the ventral roots do not emerge in linear arrangement but rather have their exit irregularly through a considerable surface of the ventrolateral part of the cord.

INTERNAL STRUCTURE OF CORD

Section of the cord (Figs. 60 and 61) shows it to be made up of an outer zone of *white matter* and an inner H-shaped mass of *gray matter*. The white matter occurs in the form of three longitudinal columns of nerve fibers, chiefly myelinated, extending the length of the cord. Each column or funiculus consists of a number of functionally distinct bundles of nerve fibers known as *fiber tracts*. The gray matter actually is a fluted mass of nerve cells and fibers, also extending

fissure. Posteriorly it is attached to the posterior median septum. There is an external layer of longitudinally arranged fibers which gives a denser and thicker texture to the pia of the cord than the pia of the brain possesses. The blood vessels of the cord lie between the two layers of pia. Anterior to the anterior-median septum the pia is characterized by a longitudinal band of glistening white fibrous tissue, the *linea splendens*. This is continuous below with the filum

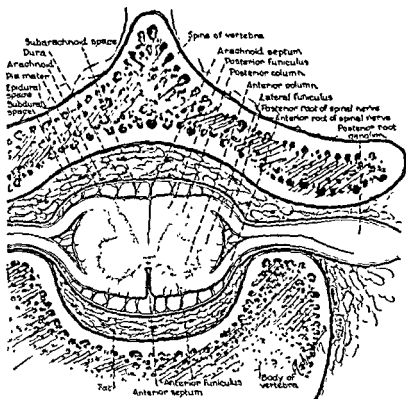


FIG 59—SECTION OF PORTION OF VERTEBRA AND SPINAL CORD SHOWING MENINGES

terminale. At the foramen magnum the spinal pia is continuous with that of the brain. The pia constitutes the floor of the subarachnoid space.

THE SPINAL CORD

Embryologically the cord (Fig. 57) is a tube, but in the adult the lumen, represented by the central canal, is relatively very small. The adult cord is flattened slightly on its anterior and posterior surfaces. It has two swellings or *intumescencia*, one in the lower cervical region and one in the lumbar region. These are produced by the increased numbers of entering nerve fibers at these levels, the fibers being those of the brachial and the lumbosacral plexuses. Throughout its length, however, the diameter of the cord is much less than that of the spinal canal in which it lies. It is thus surrounded by a space, already described as the subarachnoid space, save at the ligaments by which it is attached

Solitary cells are scattered through the posterior column. A group of cells in the lateral part of the base of the posterior column is known as the *nucleus proprius* of the posterior column. Together with the cells of the reticular

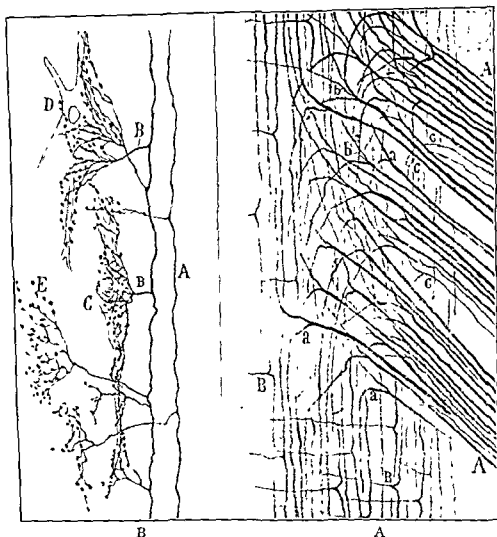


FIG. 62.—A. BIFURCATION OF DORSAL ROOT FIBERS WITHIN CORD AND B. RELATION OF COLLATERALS TO CELLS OF POSTERIOR GRAY COLUMN.

B is more highly magnified than A. (After Cajal.)

A A, posterior root fibers; B, posterior column of spinal cord, with collateral fibers; a, b, bifurcation of sensory fibers; c, fine fibers which bifurcate in Lissauer's zone.

B A, unmyelinated fibers; B, short collaterals; C, D, large cells at margin of gelatinous substance of Rolando, E, terminal branches with marked varicosities.

formation, these cells are regarded as the integrating mechanism of spinal reflexes.

NUCLEUS DORSALIS—The medial part of the base of the posterior column in the thoracic and lumbar cord is occupied by a distinct group of large cells known as the *dorsal nucleus* or *column of Clarke*. It begins at the level of the 8th cervical or the 1st thoracic segment of the cord and continues to the 2nd or 3rd L. segments. In the monkey it extends to the lower lumbar segment. It attains its largest size in the 12th thoracic and diminishes above the 9th thoracic segment.

the length of the cord. For convenience of description it is divided, on each side, into *posterior* and *anterior columns* or *horns*. The two sides are connected by the *gray commissure*, which crosses the midplane and surrounds the central canal. Ventral to the central canal there is an *anterior white commissure*, made up of myelinated nerve fibers. These arise from cells in the gray matter and cross to the ventral and lateral funiculi of the opposite side.

The *POSTERIOR COLUMNS* are divided for descriptive purposes into a pointed *apex*, an expanded *caput*, and a constricted *cervix*. The substance of the apex has a translucent appearance in the fresh cord, and is known as the *gelatinous substance of Rolando* (Fig. 63). It is composed of nerve cells and neuroglia.

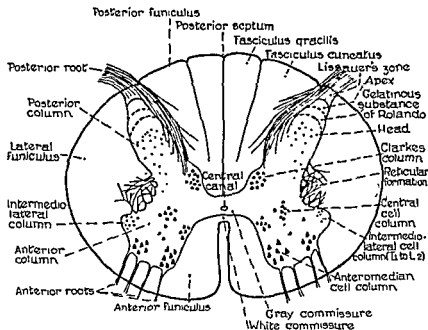


FIG 61—DIAGRAM OF CROSS SECTION OF SPINAL CORD, SHOWING REGIONS OF WHITE AND GRAY SUBSTANCE.

The nerve cells are arranged in three zones, namely, an external or marginal zone of large fusiform cells, an intermediate zone of small fusiform cells, and a ventral zone of stellate cells and of Golgi type II cells. The axons of cells from the gelatinous substance pass, for the most part, into the dorsal and lateral funiculi. They ascend or descend in the cord, or divide into ascending and descending branches. Some reach the brain, others end in the gray matter of higher or lower segments of the cord. Bundles of such fibers between different levels of the cord are known as the *ground bundles*, *spinothalamic fibers* or *fasciculi proprii*. The fibers which do not cross are known as *association bundles*, those which cross as *commissural fibers*. Axons of the Golgi type II cells connect with adjacent nerve cells in the gray matter.

RETICULAR FORMATION—Lateral to the head and the neck of the posterior column is a zone of intermingled nerve cells and fibers known as the *reticular formation* (*formatio reticularis*). This is most marked in the cervical cord.

pretty closely to the cervical and lumbar enlargements of the cord. Their cells give rise to the motor fibers to muscles of the arm and leg. These motor fibers to voluntary muscles of the body are known as the *lower motor neurons*.

LATERAL COLUMN.—Most marked in the thoracic region of the cord there is a *lateral column* of gray matter, in addition to the anterior and posterior columns already described. It can however be followed throughout the length of the cord. In the thoracic cord there is an *intermediolateral column* of cells. These cells are much smaller than the ventral horn cells. They are stellate or fusiform. Their axons, for the most part, emerge from the cord with the ventral roots, to reach the sympathetic chain ganglia via the white rami. They constitute the *preganglionic fibers* of the thoracolumbar autonomic system, supplying part of the motor innervation to the viscera. This column of cells corresponds in distribution to the body segments having white rami communicantes.

REFLEX MECHANISMS

The first movement which can be evoked in early salamander larvae by tactile stimulation of the skin is a simple avoiding reaction. This takes the form of turning the head away from the side stimulated by contraction of the upper trunk myotomes of the opposite side. At a slightly later stage of development this response is followed by a "coil reaction." The response begun as just described is continued tailward by contraction of successive myotomes. By the time the more caudal myotomes in this series have contracted, an impulse has been transmitted to the more rostral myotomes of the side originally stimulated, causing them to contract so that the larva assumes the form of an elongated S. Still later in development the wave of contraction progresses tailward on the side originally stimulated, and a new wave of contraction begins with the rostral myotomes of the opposite side. When these alternate waves of contraction follow each other rapidly enough, swimming movements result.

Histological study of the nervous system of larvae tested for such responses has enabled Coghill to correlate the movements noted with the neural mechanism of the cord at different stages of differentiation. Primitive sensory neurons (Rohon-Beard cells) which are located in the dorsal part of the larval cord give off peripheral processes. These divide in such a manner that one branch passes to the skin for cutaneous reception and another passes to the myotomes. The latter is stimulated by the contraction of the myotomes, producing proprioceptive impulses.

Another branch from each Rohon-Beard cell ascends within the cord and connects with a chain of neurons by which the impulses brought in by the two peripheral processes are transmitted to the cephalic part of the cord. In this region of the cord there are cells with commissural fibers. The impulses cross through these fibers and are transmitted caudalward, through a series of neurons, to the successive myotomes. By the entrance of sensory fibers into successive segments of the cord there is formed a primitive ascending fiber tract composed

The axons of its cells pass into the lateral funiculus to ascend as the dorsal spinocerebellar tract. The cells are oval or pyriform.

A CENTRAL GELATINOUS SUBSTANCE around the central canal possesses a few stellate or fusiform cells whose axons pass into the lateral funiculus of the same or the opposite side.

The ANTERIOR COLUMN of gray matter contains the largest cells in the nervous system, although there is much variation in size. These cells are arranged in longitudinal columns which in cross section of the cord appear as cell groups. The axons of the large-celled columns form the ventral nerve roots to the

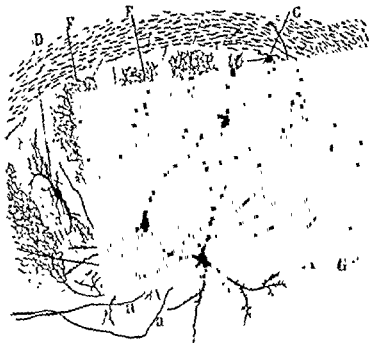


FIG. 63.—CELLS IN GELATINOUS SUBSTANCE OF ROLANDO. (From Cajal)

A, cells of the head of the posterior horn, *B*, *C*, *D*, cells of the gelatinous substance of Rolando; *E*, deep collaterals to substance of Rolando; *F*, branching nerve terminals from the deep collaterals; *a*, axon; *b*, longitudinal nerve terminations of the tip of the posterior horn.

muscles of the body. In the medial part of the anterior column is found the anteromedial column of cells, extending throughout nearly the entire length of the cord. According to Bruce it is well marked in C4, C5, C8 to L4, and S2, S3 and S4. It disappears in L5 and S1. The posteromedial column consists of small cells lying posteriorly and is represented in part of the cervical cord, in Th 1-12 and L1, but not in L5, S1, S2 or below S4. These two columns are believed to supply the muscles of the trunk and neck. The anterolateral column of cells is found in C4 to C8 and in L2 to S2. The posterolateral column is found in C4 to C8 and in L2 to S3. The retroposterolateral column is restricted to C8, Th1, and S1, S2, and S3. The central column is limited to L2 to S2. These several columns correspond, in their distribution,

the spinal nerves through the cardiac and pulmonary plexuses, the splanchnic nerves, the mesenteric plexuses, and the pelvic nerve. On reaching the cord they form reflex arcs with visceral efferent neurons, chiefly, but there is evidence of a visceral ascending pathway within the cord which appears to have the primitive pattern of relays of neurons. This is located in the lateral funiculus.

DORSOLATERAL TRACT.—The somatic afferent fibers become segregated, as already noted, into a medial division (Fig. 66) of myelinated fibers and a lateral division, chiefly unmyelinated, but with some small unmyelinated fibers intermingled. The lateral division enters the *dorsolateral tract* of Lissauer (Figs. 66-70 and 74), while the medial division enters the dorsal funiculus. On entering the cord the fibers of the lateral division bifurcate into ascending and descending fibers, the latter descending one segment while the ascending fibers continue upward one or two segments. Both rami eventually penetrate into the dorsal column and by collaterals and by terminal arborizations form synaptic connections with neurons therein. The terminal fibers synapse with neurons whose axons cross in the ventral white commissure to enter the lateral *spinothalamic tract* (Figs. 66 and 74) of the opposite side of the cord. The collaterals and descending rami are regarded as forming synaptic connections with spinal neurons of reflex arcs. The study of action currents in nerve fibers by means of the cathode ray oscillograph has enabled Clark, Hughes and Gasser to definitely relate pain stimuli, which could be localized, to small myelinated fibers of the nerves. Diffuse pain, on the other hand, was associated with small, unmyelinated fibers. These facts fit into the experimental and clinical evidence that Lissauer's tract conveys pain sensation.

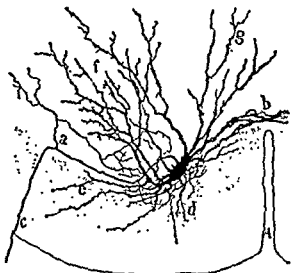


FIG. 64.—MOTOR CELL IN ANTERIOR GRAY COLUMN.

a, recurrent collateral from an axon; b, commissural dendrites; c, axon; d, dendrites extending into anterior part of spinal cord. Chick embryo. Golgi method. From Cajal, *Histology*, Wm. Wood & Co., Baltimore, 1933

The **LATERAL SPINOTHALAMIC TRACT** is known from clinical evidence to transmit stimuli of pain and temperature. The fibers, which are myelinated, extend from their level of origin without interruption, to the thalamus (Fig. 74). The tract is therefore increased in size at each successively higher body segment by entering fibers. Injury to this tract results in loss of pain and temperature sensations from the opposite side of the body, beginning, as a rule, two segments below the level of the lesion.

The medial divisions of the dorsal roots enter the dorsal funiculus directly.

of relays of neurons. In the ventral part of the larval cord a primitive motor tract is also formed of relays of neurons. In *Amblystoma* larvae the arrangement of the latter is such as to favor a progressively downward contraction of myotomes by delay in transmission at each synapse. The entire pattern, however, is one for total reaction of the organism rather than for local reaction. As development of the larva continues, local reflex arcs become individuated from the total reaction mechanism. Thus as the legs are elaborated, local leg reflexes become possible by a gradual process of modification in the cord involving the differentiation of new neurons.

In mammals, Windle, studying cat embryos, has held that local reflexes, rather than total reactions, appear first. Angulo, with rats, and Hooker, with human fetuses, find total reaction first and individuated reflexes later. These observations have an important bearing on our conceptions of the growth and functioning of the nervous system.

As additional receptors are differentiated, other ascending fiber tracts are added within the cord and brain stem. The ascending fibers tend to increase in length, so that in man some extend all the way from the level of entrance as far as the medulla oblongata. Others end within the cord at various levels above the segment of entrance, relaying their stimuli to secondary neurons which aggregate to form fiber tracts. Most of these continue without further interruption to the brain stem. There are indications, however, that some of the functional tracts, even in mammals, consist of a chain of neurons.

The brain assumes an increasingly dominant control over the spinal cord mechanisms in man. This is accomplished by growth into the cord of descending fiber tracts from various brain centers, to be described. The spinal cord thus consists of the gray matter, with its groups of neurons, and the white matter, made up of nerve fibers. The latter may be divided into four categories, namely, (1) fibers from the spinal nerves (Fig. 62); (2) ascending fibers which originate in the cord and reach the brain stem; (3) descending fibers from the brain to various levels of the cord; (4) fibers from one level of the cord to another.

FIBER TRACTS

ASCENDING TRACTS

The spinal nerves, with their components of somatic and visceral afferent and efferent fibers, break up into dorsal and ventral roots on approaching the cord. The ventral roots contain the efferent fibers (Figs. 64 and 65), both somatic and visceral. They are distinguishable histologically by differences in size. They enter the cord to attach to their nerve cells in the ventral column and in the intermediolateral column, respectively. The dorsal roots also are composed of two main categories of fibers, namely, general visceral afferents, from the viscera, and general somatic afferents, chiefly from the skin. The visceral afferents reach

gracilis. The nucleus in which the fibers terminate is known as the *nucleus of the fasciculus gracilis*. It is located in the lower part of the medulla oblongata.

FASCICULUS CUNEATUS (Figs. 66 and 75).—The fibers of the dorsal funiculus become arranged in layers in such fashion that those entering from the sacral nerves have the most medial position, lying against the dorsal median septum. Those entering from the lumbar nerves form the next layer, etc., so that in progressively higher levels of the cord the ascending fibers of the successive segments assume a more and more lateral position. From the 5th thoracic segment and upward the ascending rami in the dorsal funiculus constitute a distinct lateral bundle known as the fasciculus cuneatus. Its fibers terminate in the *nucleus*

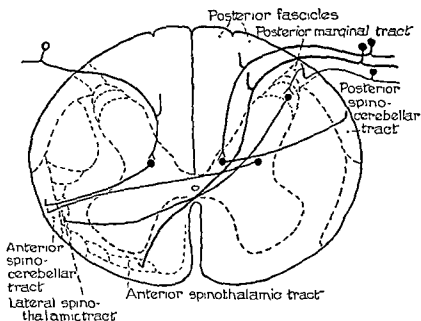


FIG. 66.—DIAGRAM OF CROSS SECTION OF SPINAL CORD SHOWING CONNECTIONS OF DORSAL ROOT FIBERS WITH VARIOUS ASCENDING FIBER TRACTS

fasciculus cuneatus, in the lower end of the medulla oblongata, lateral to the nucleus fasciculus gracilis.

These long sensory fibers have to do with two types of conscious stimuli only, according to Stopford. One is recognition of the position and passive movement of joints. The second is recognition of two points stimulated at the same time, i.e., compass test.

FASCICULUS INTERFASCICULARIS—The descending rami of the medial division fibers terminate in the gray substance of the posterior column. Some pass directly to the posterior column, others first descend a short distance in the interfascicular fascicle or *comma bundle* of Schultze. Still others descend in the *septo-marginal fasciculus* before turning into the gray substance. These two fasciculi also contain fibers which have their origin from cells in the cord.

SPINAL LEMNISCUS—This is a term applied collectively to the ascending fibers from spinal cord to the thalamus which convey pain, temperature and

Several functional types of fibers are represented. They also bifurcate into ascending and descending rami. The ascending rami of one functional type, not distinguishable histologically from others, however, since all are large myelinated fibers, pass upward a number of segments within the cord, giving off collaterals to the gray matter in their course, before the terminal processes also pass into the gray matter to end there in relation to dorsal column cells.

THE VENTRAL SPINOTHALAMIC TRACT.—The cells of the posterior column give rise to fibers, also myelinated, which cross through the ventral white commissure to the other side of the cord and take up their position in the ventral funiculus as the ventral spinothalamic tract (Fig. 66). The fibers then turn upward to terminate in the thalamus (Fig. 73). Injury to the cord which affects

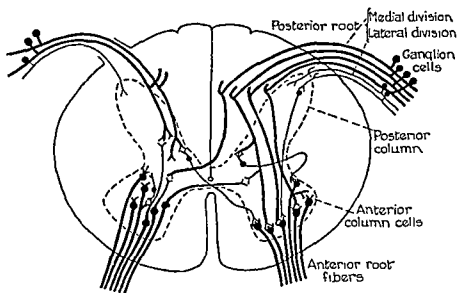


FIG 65.—REFLEX ARCS IN SPINAL CORD.

this tract results in failure of tactile and pressure stimuli to reach the brain. Again the skin area affected is on the side of the body opposite to that of injury to the cord. There is evidence that part of this tract is formed of relays in the cord and brain stem, constituting a *spinoreticular tract*. The ventral spinothalamic tract is also augmented at each successively higher level by fibers from each segment of the cord. It conducts impulses of lightest touch or pressure and of localization of touch (Stopford).

FASCICULUS GRACILIS.—Many of the ascending fibers of the median division of the dorsal root ascend the length of the cord, from the level of entrance, to terminate in a nucleus at the lower end of the medulla oblongata (Figs 66 and 75). These long ascending fibers form two bundles in the dorsal funiculus of the cord. Those from the lower part of the cord and upward to about the 5th thoracic segment form a bundle placed medially which is called the fasciculus

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chiefly on the opposite side, but to some extent on the same side. The crossed fibers reach the ascending bundle through the anterior commissure. The tract enters the cerebellum through the superior cerebellar peduncle and ends in the anterior lobe of the corpus cerebelli. This is phylogenetically the oldest of the spinocerebellar tracts. It is included with the spinotectal and the lateral spinothalamic tracts as *Gowers' fasciculus*.

The DORSAL SPINOCEREBELLAR TRACT of Flechsig arises from cells (Fig. 76) of the dorsal column of Clarke. It is usually described as homolateral, but Pass, in the cat, describes it as derived chiefly from cells of the opposite side of the

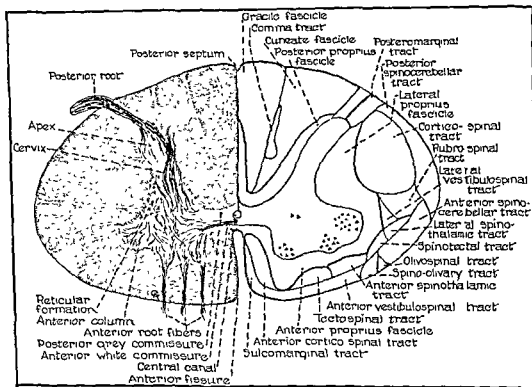


FIG. 68.—LOWER CERVICAL SPINAL CORD

cord. The fibers reach the lateral funiculus and occupy a superficial zone between the ventral spinothalamic tract and the posterolateral sulcus. They enter the cerebellum through the restiform body and are distributed to the anterior lobe and part of the posterior lobe of the corpus cerebelli.

The INTERMEDIATE SPINOCEREBELLAR TRACT has been described by Pellizi and by Beck. It is closely associated with Flechsig's tract and has been regarded as part of the latter. The spinocerebellar paths carry proprioceptive stimuli which do not come to consciousness but have to do with muscular coördination and related functions.

The SPINOTECTAL TRACT arises from cells in the posterior gray column. The fibers cross to the opposite side of the cord and ascend in the lateral funiculus to reach the tectum of the midbrain. It is apparently a correlation pathway.

touch sensibility, as already described. The evidence for separation of the cord pathways of pain and temperature from those of touch and pressure is chiefly clinical. For example, syringomyelia involves destruction of the cord around the central canal in varying degree. Sometimes the anterior white commissure is destroyed, resulting in loss of pain and temperature sensations on the opposite side of the body below the level of the lesion. Touch and pressure sense may remain intact, due to the fact that the central rami of the posterior root fibers of the spinal nerves ascend for many segments on their side of entrance

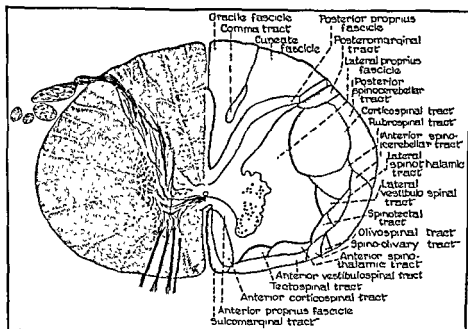


FIG 67.—SECTION OF SPINAL CORD IN UPPER CERVICAL REGION.

Diagram on right hand side shows fiber tracts and cell groups. Ascending fiber tracts blue, descending tracts red, ground bundles yellow.

into the cord before relaying their impulses to the secondary fibers which cross and become the anterior spinohthalamic tract. Lesions below the cervical region of the cord, if confined to one side, have little or no effect on touch and pressure sensation, indicating a double pathway, one through the posterior funiculus and one through the lateral funiculus, for these sensations. The posterior funiculus contains the fibers for *epicritic sensibility* which is a more highly refined form of cutaneous sensibility than is carried by the fibers of the anterior spinohthalamic tract. The *epicritic fibers* are regarded as more recent, phylogenetically, than those of the lateral funiculus.

SPINOCEREBELLAR TRACTS (Figs. 66 and 77).—Fibers from the posterior column of the gray substance pass to the superficial part of the lateral funiculus and turn upward to end in the cerebellum. The *anterior spinocerebellar tract* arises from cells in the posterior gray column and in the intermediate column,

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in the gray matter, ascend or descend a varying number of segments and terminate in relation to cells at other levels of the gray substance. Fibers connecting the nearer segments lie close to the gray substance while those connecting more distant parts of the cord are crowded farther away. Some fibers of this group intermingle with ascending or descending fibers whose origin is not in the cord. Thus the *comma tract* of Schultze, in the dorsal funiculus, already stated as made of mixed fibers, includes proprius fibers with the descending rami of spinal root fibers. This is also true of the *septomarginal tract*. The *sulcomarginal tract*, in the ventral funiculus, consists of ventral proprius fibers and fibers from the medial longitudinal bundles of the medulla oblongata.

The proprius fibers make possible reflex arcs between the different segments of the cord. They undoubtedly play an important rôle in correlating its activities. With their cell bodies and related processes they constitute the intercalated neurons between dorsal and ventral root elements in many of the spinal reflex arcs.

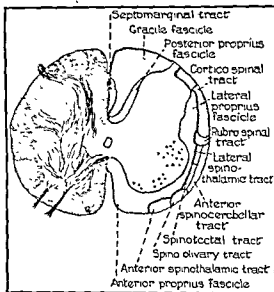


FIG. 71.—SACRAL SPINAL CORD.

DESCENDING TRACTS

A number of fiber tracts having their origin in various parts of the brain descend into the cord and terminate in its gray substance. Some of the fibers form synaptic connections directly with ventral root neurons, either somatic or visceral motor. The majority, however, appear connected by one or more intercalated neurons. Many tracts of different functional significance are connected in this way to the final motor neurons whose axons lead to the effector organs. The final motor neuron thus receives the correlated stimuli from many parts of the brain and cord, hence it has been called by Sherrington "the final common path."

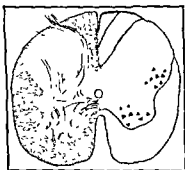


FIG. 72.—LOWER SACRAL SPINAL CORD.

The corticospinal tract or pyramidal tract conducts voluntary motor impulses from the cerebral cortex to the various levels of the cord. It has its origin from large pyramidal cells (Betz cells) in the precentral gyrus. These cells are so arranged that fibers from specific regions of the gyrus pass to specific groups of muscles. The tract passes through the ventral part of the brain stem into

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The SPINO-OLIVARY TRACT also has its origin from cells of the posterior gray column. The fibers cross and ascend to the inferior olive of the medulla oblongata.

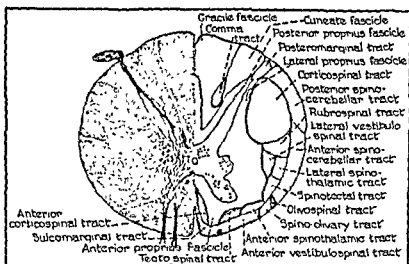


FIG. 69—UPPER THORACIC SPINAL CORD.

GROUND BUNDLES OF PROPRIOUS TRACTS, already mentioned, are collected into three principal masses, namely, the *posterior*, the *lateral*, and the *ventral* ground

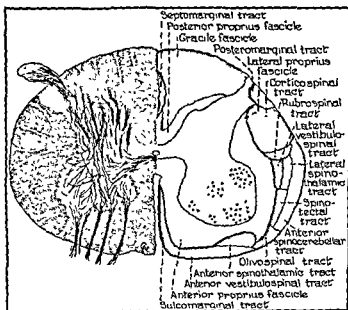


FIG. 70—LUMBAR SPINAL CORD.

bundles, one for each funiculus of the cord. They occupy a position adjacent to the gray substance in their respective funiculi. The fibers arise from cells

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gray column. There is evidence that fine terminal *boutons* from at least some of these fibers end directly on ventral horn cells and their dendrites. Usually they are regarded as ending on cells intercalated between them and the cells of the motor root fibers.

The VENTRAL CORTICOSPINAL TRACT (VENTRAL PYRAMIDAL TRACT) includes the fibers which continue directly into the ventral funiculus of the cord without

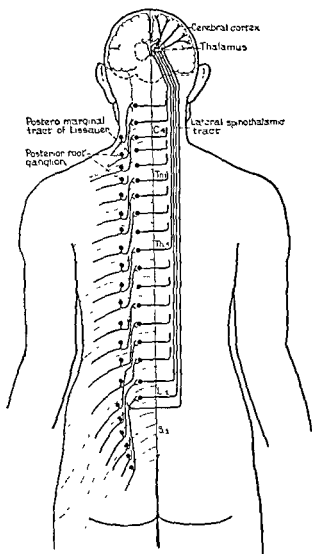


FIG. 74.—DIAGRAM OF THE PATHWAY FOR PAIN AND TEMPERATURE SENSATION.

The afferent neurons of the 1st order ascend two or three segments in the spinal cord before making synaptic connections with the neurons of the 2nd order. The latter cross to the opposite side of the cord and ascend as the lateral spinothalamic tract.

decussation at the lower end of the medulla oblongata. They form a small tract in the ventral funiculus. This can be followed usually into the upper thoracic cord, but there is much variation in its extent in different individuals. It appears to be a new tract phylogenetically, having been found only in higher

the cord. At the level where the medulla oblongata merges with the cord it divides into a *lateral* and a *ventral corticospinal tract*, about four-fifths of the fibers crossing as the *decussation of the pyramids*.

The LATERAL CORTICOSPINAL TRACT (LATERAL PYRAMIDAL TRACT) (Figs. 67-72 and 225) is made up of the crossed and uncrossed fibers and forms a

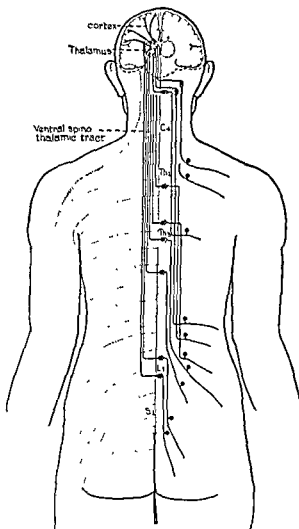


FIG. 73—DIAGRAM OF THE PATHWAY FOR TACTILE SENSATION.

The afferent neurons of the 1st order ascend a varying number of segments in the spinal cord before making synaptic connections with the neurons of the 2nd order. The latter cross to the opposite side of the cord and ascend as the ventral spinothalamic tract.

large tract in the upper part of the lateral funiculus. It is the larger and more important of the two pyramidal tracts, but gradually decreases in size as it descends. It is recognizable as a distinct bundle as far as the fourth sacral segment. The uncrossed fibers pass directly from the pyramids into the tract of the lateral funiculus. It gives off terminal fibers and collaterals which enter the anterior

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When the upper motor neuron is injured, as in lesions of the corticospinal tracts, the voluntary muscles lose the power of controlled movement. Reflexes of spinal origin below the level of the lesion, however, remain intact. Thus the *flexion reflex* of the lower extremity is produced by stimulating the skin, especially of the foot. The flexor muscles of hip, knee and ankle contract, while the extensors relax in a protective movement involving many segments of the cord. In the *Babinski reflex* the flexor movement of the lower extremity is accompanied by an extension of the toes, which occurs when the corticospinal tract is injured.

Lesions of the lower motor neuron, such as severing the anterior roots or injury to the anterior column cells, as for example, by the virus of poliomyelitis,

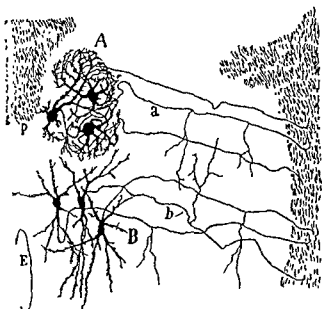


FIG. 76—CELLS OF CLARKE'S COLUMN. (From Cajal.)

A, column of Clarke, *B*, nucleus of intermediate gray substance; *E*, central canal, *a*, axons from cells of Clarke's column, showing collaterals; *b*, axons from cells of the intermediate gray substance. Newborn mouse, Golgi method.

causes loss of all reflexes of the muscles involved, as well as loss of voluntary movements. The muscles gradually waste away to small size.

The **RUBROSPINAL TRACT** (TRACT OF MONAKOW) (Figs. 67-72 and 226) has its cells of origin in the red nucleus of the midbrain. The fibers cross in the ventral tegmental decussation and continue into the cord. The tract lies in the lateral funiculus and is described as reaching the sacral cord. The fibers enter the gray matter at successive levels, ending in relation to the motor cells of the anterior column.

The **TECTOSPINAL TRACT** (TRACT OF LÖWENTHAL) (Figs. 67-72) arises in the roof (tectum) of the midbrain. The fibers cross, in part, in the dorsal tegmental decussation and descend in the ventral funiculus as far as the upper thoracic cord. They end directly or through intercalated neurons, in relation

apes and man. Most of the fibers cross, a few at a time, in successive segments of the cord, to end in relation to ventral horn cells. There is evidence, however, that many terminate on the side from which they have their origin.

The cells and fibers of the corticospinal tracts form the first link in the

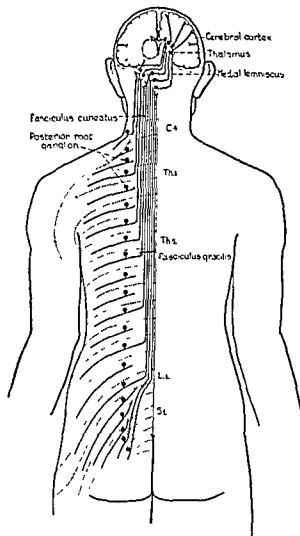


FIG. 75—DIAGRAM OF FASCICULUS GRACILIS AND FASCICULUS CUNEATUS CONNECTIONS.

The afferent neurons of the 1st order ascend in the dorsal funiculus of the spinal cord, on the side of entrance, to the nucleus fasciculus gracilis and nucleus fasciculus cuneatus respectively, before relaying to neurons of the 2nd order in these nuclei. Fibers from these nuclei cross in the medulla oblongata and form the medial lemniscus, which reaches the thalamus

voluntary motor pathway They are called the *upper motor neurons*. The final link is formed by the motor cells of the anterior column and their anterior root fibers. These constitute the *lower motor neurons*. Connection between the two is made in the gray substance either by direct synapse or through the mediation of intercalated neurons of the cord.

thalamic tract. They extend to the lower lumbar or sacral segments, giving off segmental fibers throughout its course which end in the anterior gray column. This tract serves equilibratory reflexes.

A LATERAL VESTIBULOSPINAL TRACT, arising from cells in Deiter's nucleus and in the spinal vestibular nucleus, and descending in the lateral funiculus of the cord on the same side, has been described. The fibers intermingle with those of the rubrospinal tract. This tract has not been well established.

The RETICULOSPINAL TRACT arises from small groups of cells and from scattered cells in the reticular formation of the midbrain and upper part of the pons. According to Papez there is an anterior and a lateral reticulospinal tract. The first named passes, without decussation, through the medulla oblongata into the anterior funiculus of the cord. The lateral tract fibers decussate and enter the lateral funiculus of the cord. Both are regarded as ending, directly or indirectly, in relation to motor neurons of the anterior gray and the intermediolateral columns. Some of the reticulospinal fibers clearly connect with cells whose axons form preganglionic fibers of the thoracic autonomic system. They take part in vasomotor and other reflexes of visceral type.

While the fiber tracts are represented as occupying circumscribed areas in the spinal cord, there is actually considerable intermingling of fibers belonging to tracts of different functional connections, especially at the margins of the various bundles. Areas actually overlap to a considerable extent, although shown in figures of cross sections of the cord, as a rule, as having definite boundaries.

CLINICAL INTERPRETATION

SOME LESIONS OF THE SPINAL CORD

Complete section of the spinal cord in man, if care is taken to avoid infection, results in the following series of phenomena:

- 1 Spinal shock, characterized by inability of the severed segments of the spinal cord to perform reflexes, or to maintain muscle tone. The sphincters of the bladder and rectum become strongly contracted as early as the third day after injury, but the skeletal muscles show flaccid paralysis and complete loss of tone below the level of injury. There is also complete loss of sensation and voluntary motion below the level of injury, with retention of urine and feces, due to contraction of the sphincters. The severed part of the cord is rendered almost non-functional, illustrating its dependence, in man, on the higher centers.

2. After one to three weeks the shock passes away and the reflex functions of the cord gradually return. The first to appear is the flexor reflex from stimulation of the sole of the foot by means that in a normal individual would produce pain. The earliest response is adduction and flexion of the toes, but with increased recovery of function in the cord, such a stimulus elicits a flexor reflex consisting of extension of the toes (the Babinski reflex) accompanied by flexion of the

to the motor neurons of the anterior column. A *lateral tectospinal tract*, made up of fibers of the above bundle, which on reaching the cord enter the lateral funiculus, instead of the ventral, has also been described. These tracts serve optic and auditory reflexes.

The **OLIVOSPINAL TRACT (HELWEG'S BUNDLE)** (Figs. 67-72) also called the bulbospinal tract, arises in the medulla oblongata. Its exact origin is not clear, although it is usually described as in the inferior olive. It descends in the

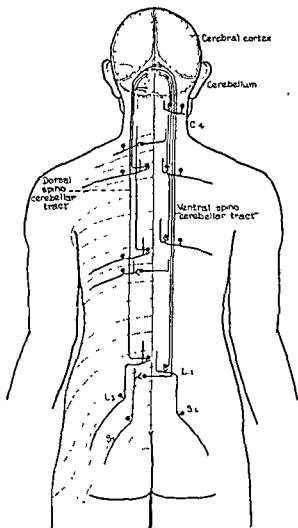


FIG 77.—DIAGRAM OF SPINOCEREBELLAR TRACTS AND CONNECTIONS.

lateral funiculus, occupying a position lateral to the anterior gray column, as far as the lower cervical and possibly upper thoracic segments of the cord. The termination of its fibers is obscure.

The **VESTIBULOSPINAL TRACT** (Figs. 67-72 and 129) has its origin in the lateral vestibular nucleus of the medulla oblongata. The fibers descend in the ventral funiculus, intermingled with ascending fibers of the ventral spino-

thalamic tract. They extend to the lower lumbar or sacral segments, giving off segmental fibers throughout its course which end in the anterior gray column. This tract serves equilibratory reflexes.

A LATERAL VESTIBULOSPINAL TRACT, arising from cells in Deiter's nucleus and in the spinal vestibular nucleus, and descending in the lateral funiculus of the cord on the same side, has been described. The fibers intermingle with those of the rubrospinal tract. This tract has not been well established.

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knee and ankle, adduction of the thigh and flexion of the hip, *i.e.*, a marked avoiding reaction. In some cases the opposite limb may also be involved. Gradually there is some return of extensor reflexes and knee-jerk can be obtained.

3. The visceral reflexes return after the flexor reflexes. The bladder and rectum may begin to empty themselves at certain degrees of distention if care has been taken in earlier stages of recovery to prevent *overdistention*. Stimulation of the genitals causes erection, which may be accompanied by emission, and by movements of coitus.

Hemisection of the spinal cord results in the following combinations of loss of sensory and motor functions, known as Brown-Séquard's syndrome:

1. Loss of voluntary muscular movement on the side of the lesion, beginning immediately below the level of injury. This is accompanied by increased muscle tone and exaggerated tendon reflexes (*e.g.*, knee-jerk) in the affected portions of the body. Such motor loss, with increased muscle tonus and exaggerated reflexes is known as spastic paralysis. It is accompanied by little or no wasting of the muscles affected. It is due to injury to the upper motor neuron of the voluntary motor pathway. The lower motor neurons are intact, making possible muscular reflexes below the lesion. These are exaggerated because the control normally exercised by the upper motor neuron is removed.

2. Loss of proprioceptive (muscle, joint and tendon) sense, with or without diminution of tactile sense below the level of lesion on the same side.

3. Loss of pain and temperature sense on the opposite side of the body, beginning two segments below the level of the lesion.

4. Increased temperature and flow of blood on the same side due to paralysis of vasomotor fibers.

5. No sensory or motor disturbances are found in other parts of the body. There are many variations of this syndrome, depending on the level of injury, its extent, etc.

DISSOCIATED ANESTHESIA.—Syringomyelia is a pathological condition of the spinal cord marked by excessive proliferation of neuroglia in the central gray substance, accompanied by formation of cysts. In this disease the fibers of pain and temperature, which cross in the white commissure, undergo degeneration, interrupting the pain and temperature pathway of the lateral spinothalamic tract.

The fibers of touch and pressure which cross to the ventral spinothalamic tract are also injured. This type of sensibility, however, is also served by fibers in the dorsal funiculus which do not relay until they reach the medulla oblongata. Hence pain and temperature sensibility may disappear in areas of skin supplied by nerves one or two segments below the part of the cord affected, while touch and pressure sensibility remains virtually intact.

Hemorrhage within the spinal cord (*hematomyelia*) or tumors may destroy parts of the cord, with similar dissociation anesthesia.

Posterior spinal sclerosis or *tabes dorsalis* is characterized by a progressive degeneration of the posterior funiculi and of the posterior roots of the spinal

nerves. There result in varying degrees, according to the amount of degenerative change: (1) incoördination of the muscles, especially of the extremities, from failure of proprioceptive stimuli to reach the coördinating centers of the brain; (2) reduced muscle tone and deep reflexes, also from failure of proprioceptive stimuli to function; (3) loss of tactile discrimination, although touch recognition is not lost since the fibers concerned cross and ascend in the ventral spinothalamic tract; (4) pain and temperature senses are unaffected.

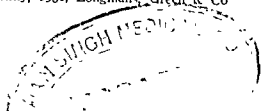
Primary lateral sclerosis is due to degenerative changes in the lateral pyramidal tracts, usually on both sides. The degeneration may begin at any level of the spinal cord but rarely affects the cervical region. It results in bilateral spastic paralysis of both lower extremities, characterized by increased muscle tone, exaggerated tendon reflexes (e.g., knee-jerk), and loss of voluntary control of the muscles affected. Abnormal reflexes, such as the Babinski, appear.

There is no atrophy, loss of contour, or degeneration reaction of the affected muscles. The absence of this reaction of degeneration, together with the exaggerated reflexes and increased muscle tone, indicate that the lower motor neurons are not affected. There are no sensory effects in lateral sclerosis. The motor effects are due to involvement of the upper motor neurons.

In *combined sclerosis* primary lateral sclerosis of the pyramidal tract is combined with degeneration of the sensory fibers in the dorsal funiculus. This results, in addition to the motor disturbances of lateral sclerosis, in the sensory and reflex losses characteristic of posterior spinal sclerosis.

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THE SPINAL CORD AND MENINGES

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CHAPTER 8

CRANIAL NERVES

The cranial nerves may be divided into two groups according to the part of the brain to which they attach. The first four pairs, lying rostral to the isthmus, are attached to the cerebrum. Those lying caudal to the isthmus are attached to the medulla oblongata. The total number of cranial nerves is usually given as twelve, following the descriptive anatomists. The studies of comparative neurologists and more detailed analysis of central connections and peripheral distribution indicates that fifteen pairs should be recognized in man, in addition to the rudimentary *nervus terminalis*.

No one of them corresponds to the spinal nerves, but several of those of the medulla oblongata correspond more closely than do the more rostral nerves. The bulbar nerves are arranged in a segmental pattern reminiscent of that in the cord, but greatly modified in man because of the special structural relations of the head and of the medulla oblongata. The functional components of the cranial nerves show various combinations of general somatic and general visceral afferent and efferent fibers, together with special fibers of each type. Special afferent fibers are due to the presence in the head region of special sensory organs, such as those of taste, hearing, etc. Special visceral efferent fibers are due to modified branchial musculature which they innervate. The muscles are those of mastication and facial expression. They are voluntary muscles, in man, not to be distinguished histologically from striated muscle elsewhere in the body. However, because they had their origin, phylogenetically, from the musculature of the gill arches rather than from the myotomes, they are regarded as special visceral muscles. The motor nerve fibers to the tongue are classed as special somatic efferent by some anatomists who regard the tongue as a special myomeric structure.

The cranial nerves (Fig. 78) are usually listed as follows: I, Olfactory; II, Optic; III, Oculomotor; IV, Trochlear; V, Trigeminal; VI, Abducent; VII, Facial; VIII, Acoustic; IX, Glossopharyngeal; X, Vagus; XI, Spinal Accessory; XII, Hypoglossal.

On the basis of comparative anatomy and the more detailed knowledge of their connections they may be listed as 1, terminal nerve; 2, olfactory; 3, optic; 4, oculomotor; 5, trochlear; 6, abducent; 7, trigeminal (sensory V); 8, masticator (motor V); 9, facial (motor VII); 10, glossopalatine or intermediate nerve of Wrisberg (sensory VII and visceral motor); 11, cochlear; 12, vestibular; 13, glossopharyngeal; 14, vagus; 15, hypoglossal; 16, spinal accessory.

CRANIAL NERVES

While recognizing the morphological relations indicated by the second list, the nerve components will be indicated for the cranial nerves, by number and name, as usually given. This is done to avoid confusion between the account presented in this book and usual anatomical and clinical usage. Because they more nearly resemble the spinal nerves the more caudal of the series will first be considered.

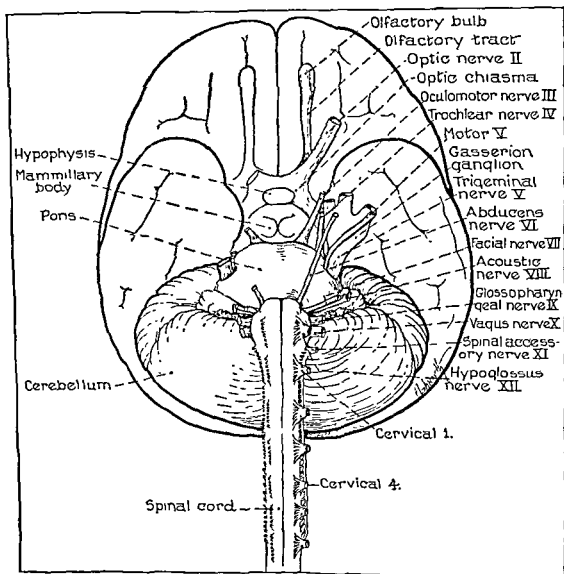


FIG 78—VENTRAL VIEW OF BRAIN SHOWING ROOTS OF THE CRANIAL NERVES

XII THE HYPOGLOSSAL NERVE arises from the ventral side of the medulla oblongata by a series of filaments which emerge between the pyramid and the olivary body. The nucleus of origin is an elongated group of cells extending anteroposteriorly in the medulla oblongata in the same relative position as the somatic motor column of the cord, but not directly continuous with the latter. It is called the *hypoglossal nucleus*. The fibers belong to the *general somatic*

CRANIAL NERVES

peduncle of the cerebellum and the olivary body. It is a mixed motor and sensory nerve, but does not have separate dorsal and ventral nerve roots, as do spinal nerves. The sensory fibers, however, are aggregated into four separate bundles which are distinct for much of their course in the solitary tract (Allen, 1924). Two ganglia, the jugular and the nodose, along the nerve, contain unipolar nerve cells which give rise to the sensory fibers. There are five functional components in the vagus, as follows:

- (1) *General somatic afferent* fibers from cells in the jugular ganglion reach the skin⁷ back of the ear through the auricular nerve.
- (2) *General visceral afferent* fibers, from cells in the nodose ganglion, pass to the lungs, the heart, the digestive tract, and the mucosa of the pharynx and larynx.
- (3) *Special visceral afferent* fibers from cells in the nodose ganglion pass to taste buds (in the infant) in the region of the epiglottis.
- (4) *General visceral efferent* fibers, from the dorsal motor X nucleus, pass to the sympathetic ganglia of the thoracic and abdominal viscera, as preganglionic fibers, relaying their stimuli to postganglionic fibers in these ganglia.
- (5) *Special visceral efferent* fibers arise from cells of the nucleus ambiguus and end in the striated branchiomeric musculature of the pharynx and larynx.

IX. THE GLOSSOPHARYNGEAL NERVE (Figs. 79 and 80) also has five functional components, corresponding to those of the vagus. Both are gill arch nerves in origin, with cutaneous and motor fibers in lower forms. The components are as follows:

- (1) *General somatic afferent* fibers, from cells in the petrous ganglion, join the posterior auricular branch of the vagus to be distributed to the skin of the back of the ear and mastoid region.
- (2) *General visceral afferent* fibers, from cells in the petrous ganglion, to the mucosa of the pharynx and part of the tongue.
- (3) *Special visceral afferent* fibers, from cells in the petrous ganglion, through the lingual branch of IX, to taste buds on posterior third of tongue.
- (4) *General visceral efferent* fibers, from the inferior salivatory nucleus, as preganglionic fibers through the motor IXth root, tympanic and small superficial petrosal nerves to the otic ganglion, where the impulses are relayed to postganglionic fibers which reach the parotid gland.
- (5) *Special visceral efferent* fibers have their origin in the nucleus ambiguus and pass through the motor IXth root and the stylopharyngeal branch of the IXth nerve to the branchiomeric striated musculature of the pharynx.

VIII. THE ACOUSTIC NERVE (Fig. 131) consists of two divisions, namely, the *vestibular* and the *cochlear*, recognized as separate nerves in the second list given at the beginning of this chapter. The cells of the *vestibular division* lie in the *vestibular ganglion of Scarpa* and the peripheral fibers pass to the ampullae of the semicircular canals and the maculae of the utricle and the sacculus. The central fibers reach the vestibular nuclei and the cerebellum. They are proprioceptors, serving equilibrium and static sense.

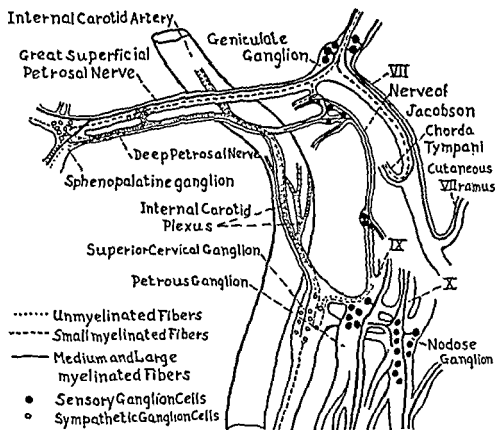


FIG. 80.—DIAGRAM OF VIIth, IXth and Xth NERVES AND SOME OF THEIR CONNECTIONS.

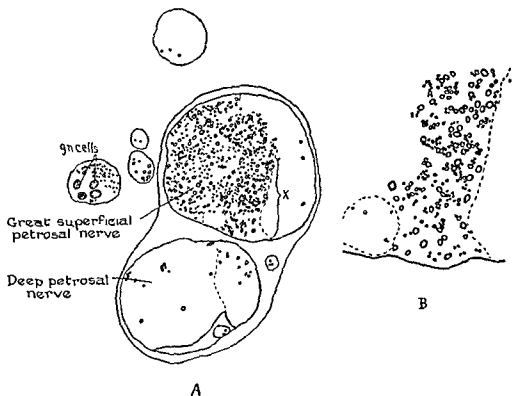
Special somatic afferent fibers have their origin from cells of the *spiral ganglion of Corti* and terminate peripherally in relation to the hair cells of the cochlea and centrally in the cochlear nuclei. These fibers carry auditory stimuli.

VII. THE FACIAL NERVE (Figs. 79, 80 and 81) belongs to the hyoid arch and like IX and X has five functional components, as follows:

- (1) *General somatic afferent* fibers, from cells in the geniculate ganglion, pass through the main trunk of the facial nerve and its cutaneous branch to the skin back of the ear and in the mastoid region, joining the corresponding rami of IX and X.

CRANIAL NERVES

- (2) *General visceral afferent* fibers, from cells in the geniculate ganglion for deep visceral sensibility, probably pass through all branches of the facial nerve.
- (3) *Special visceral afferent* fibers, from cells of the geniculate ganglion, pass through the facial trunk, the chorda tympani and lingual nerve to the taste buds on the anterior two-thirds of the tongue.
- (4) *General visceral efferent* fibers have their origin in the superior salivatory nucleus and pass as preganglionic fibers through the intermediate



A
FIG 81—SECTION OF HUMAN VIDIAN NERVE OSMIC ACID.

A, section showing areas of myelinated fibers indicated by rings of various size, and unmyelinated fibers, indicated by clear areas. *B*, the region indicated by *x* in *A*, more highly magnified.

nerve of Wrisberg, the facial trunk, the chorda tympani and the lingual nerve to the submaxillary ganglion, where the impulses are relayed by postganglionic fibers to the submaxillary and sublingual glands.

- (5) *Special visceral efferent* fibers arise from the motor VII nucleus and pass through the motor branches of the VII nerve to the mimetic muscles, derived from the musculature of the hyoid arch.

The first four named components belong to the intermediate nerve of Wrisberg. The fifth, namely, special visceral efferent, belongs to the facial proper.

VI THE ABDUCENS NERVE emerges from the medulla oblongata at the lower margin of the pons. It serves the lateral rectus muscle of the eye only. There are two components, namely:

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- (1) *Special somatic efferent* to the external rectus muscle, the fibers arising from the abducens nucleus.
- (2) *Proprioceptors*, to the external rectus muscle.

The motor fibers are considered special somatic efferent fibers because of the special function of the extrinsic eye muscles, not only in moving the eyeball which is an organ of special sense, but because fixation of vision on stationary objects is an important factor in maintenance of equilibrium.

V. THE TRIGEMINAL NERVE (Fig. 79) is primarily the sensory nerve of the face and much of the head. Its three main branches, the ophthalmic, the maxillary and the mandibular, represent the same fundamental pattern as do the palatine, chorda tympani, and main facial branches of the VIIth nerve. The ophthalmic and maxillary divisions contain only afferent fibers to the skin of the head and face, to the teeth and meninges. In addition to such sensory fibers the mandibular division contains motor fibers passing through the motor root to the muscles of mastication, which are modified gill arch muscles, hence special visceral. There are thus two functional components, in addition to *proprioceptor fibers* to the muscles of mastication, namely:

- (1) *General somatic afferent* fibers to the skin of the face and part of the head.
- (2) *Special visceral motor* fibers to the muscles of mastication.

IV. THE TROCHLEAR NERVE serves the superior oblique muscle. It has its origin from the trochlear nucleus, below the inferior colliculus of the midbrain and in the motor column. The fibers, however, emerge dorsally through the anterior medullary velum, after crossing within the brain substance. Like the abducens it contains (1) *special somatic efferent fibers* and (2) *proprioceptor fibers*.

III. THE OCULOMOTOR NERVE supplies the superior rectus, the inferior rectus, the medial rectus, the inferior oblique and the superior levator palpebrae muscles. It also supplies the smooth muscle in the interior of the eye. Its components are as follows:

- (1) *Special somatic efferent* fibers from the oculomotor nucleus to the muscles indicated.
- (2) *Proprioceptor* fibers to the muscles named.
- (3) *General visceral efferent* fibers from the nucleus of Edinger-Westphal, in the midbrain, which pass as preganglionic fibers through the oculomotor nerve and its branch to the inferior oblique muscle, then through a short branch to the ciliary ganglion, where they relay their impulses to postganglionic fibers to the sphincter muscle fibers of the iris and the ciliary muscle.

II. THE OPTIC NERVE, as described in textbooks of anatomy, is not a true nerve but corresponds more closely to a fiber tract in its structure and connec-

CRANIAL NERVES

tions. Aside from fibers which will be described in connection with the optic system, it conveys only *special somatic afferent* impulses from the retina.

I. THE OLFACTORY NERVE serves a double function, namely, testing food, which is a visceral function, and gaining information through scent of the environment, a somatic function. Many lower mammals and other vertebrates have a *vomeronasal nerve* to the vomeronasal organ (organ of Jacobson), but this is absent in man. In peripheral and central connections it is similar, in general, to the olfactory nerve but with connections to special parts of the olfactory mucosa and the olfactory bulb.

The components of the olfactory nerve are:

- (1) *Special visceral afferent* fibers from neuro-epithelial cells of the olfactory membrane to the olfactory bulb.
- (2) *Special somatic afferent* fibers with the same origin and primary destination.

The secondary and tertiary connections for the olfactory stimuli are very different, one group passing to visceral parts of the brain and the other to somatic regions. It is possible that these connections are more responsible for the two types of function shown by the nerve than are peripheral differences which have not been demonstrated.

THE NERVUS TERMINALIS, discovered by Pinkus in 1885, was found in man first by Johnston (1914). It is rudimentary in the higher vertebrates and its origin and termination as well as its function are not clear. In the lowest vertebrates it appears to be a *general somatic afferent* nerve of the skin. In mammals and man fibers and cells of sympathetic (visceral efferent) type occupy the position of the terminal nerve. A ganglion is usually found on its main trunk and scattered ganglion cells frequently occur on its main peripheral branches. In man it lies along the gyrus rectus, parallel to the olfactory tract, and enters the brain by several roots through the anterior perforated space.

CLINICAL INTERPRETATION

SOME LESIONS OF THE CRANIAL NERVES

Facial nerve paralysis (Bell's palsy) is characterized by motor paralysis of the muscles of expression. It is a lower motor neuron effect due to injury to the VIIth nerve, usually from exposure to cold. The onset is sudden and the amount of paralysis is variable. Little wasting of the affected muscles is apparent because of their small volume.

Section of the roots of the Vth nerve, including the motor root, results in complete sensory paralysis of the skin of the face, the side of the head and the frontal part of the scalp, together with motor paralysis of the muscles of mastication. In trigeminal neuralgia it is sometimes necessary to section the sensory

roots to relieve the intractable pain. After such section the taste buds in the anterior two-thirds of the tongue still function when time is allowed for recovery from the operative procedure. It is recognized that gustatory fibers from the VIIth nerve pass via the chorda tympani into the lingual nerve, which is the branch of the Vth nerve supplying the anterior part of the tongue.

The *sphenopalatine syndrome* (*Sluder's syndrome*). Irritation, as by infection, of the mucous membrane in the neighborhood of the sphenopalatine ganglion sometimes gives rise to pain which is referred by the patient to the mastoid region and which may extend to the neck and the base of the head. This is one expression of so-called referred pain. In this case it probably involves vasomotor reflexes set up by irritation of afferent fibers which pass through the sphenopalatine ganglion and reach the nuclei of the medulla oblongata through the great superficial petrosal nerve. Reflex vasomotor connections affecting the vessels of the mastoid region, the neck and the base of the head appear to be made through the reticulospinal tract. Peripheral irritation of the nasal fibers produces vasoconstriction and ischemia in the mastoid region, with accompanying pain. The cutaneous branches of the VIIth, IXth and Xth nerves also appear to be involved in bringing the pain impulses to the brain centers. Such pain can be allayed by applying a local anesthetic, as cocaine, to the sphenopalatine region or by injecting it into the skin of the mastoid region. This fact, together with vasomotor reactions from electrical stimulation of the sphenopalatine region, points to the interpretation that vasomotor phenomena are largely responsible for the sphenopalatine syndrome.

In *Gradenigo's syndrome* there is pain in the face on one side accompanied by internal squint due to paralysis of the lateral rectus muscle of the same side. The symptoms are due to infection in the tip of the petrous pyramid, involving the VIth nerve and the gasserian ganglion.

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CHAPTER 9

THE MEDULLA OBLONGATA

In the region of the medulla oblongata the embryonic neural plate undergoes modifications of form so that it does not remain a tube save at its lower part which is continuous with the spinal cord. The greater part is spread out, tapering caudally toward the cord and rostrally toward the midbrain. The narrow central canal of the cord is continuous with the broad fourth ventricle of the medulla oblongata. Rostrally the fourth ventricle continues into the aqueduct of Sylvius. The roof of the embryonic ventricle is made of a broad sheet of ependymal epithelium which extends from the rhombic lip of one side to the other.

The adult medulla oblongata (Figs. 82 and 83) in man begins at the level of the upper rootlets of the first cervical nerve and extends to the lower margin of the pons, on the anterior side. It has a length of about 25 mm. The lower part shows an *anterior median fissure*, continuous with that of the cord, but broader and deeper. It continues to the pons, where it terminates in a triangular pit called the *foramen caecum*. On each side of the fissure lies a large bundle of nerve fibers from the cerebrum, constituting the pyramids. At the lower end of the bulb these cross, forming the *decussation of the pyramids*. Interdigitating fibers from the two pyramids may be seen with a little dissection. These fibers obliterate the anterior median sulcus for 5 or 6 mm.

The *anterolateral sulcus*, continuous with the sulcus of the same name of the cord, lies lateral to the pyramids on each side. Rostrally it separates the pyramids from the *olives*, which are eminences produced on the lateral surface by the inferior olivary nuclei. The olives extend from the lower border of the pons as oblong oval swellings about 12 mm. in length. Between the olives and the pyramids, along the anterolateral sulcus, emerge the roots of the XIIth nerve, which are somatic efferent in function. Their position thus corresponds with that of ventral spinal roots.

The posterior surface of the tubular part of the medulla oblongata is marked by a *posterior median fissure*. It is continuous with the posterior fissure of the cord and ends at the obex. On each side of the rostral part of this fissure there is a swelling, the *clava*, formed by a nuclear mass in which end the fibers of the fasciculus gracilis or Goll's column. It is therefore also called the *nucleus of the fasciculus gracilis*. The posterior median fissure is especially deep between these nuclei.

roots to relieve the intractable pain. After such section the taste buds in the anterior two-thirds of the tongue still function when time is allowed for recovery from the operative procedure. It is recognized that gustatory fibers from the VIIth nerve pass via the chorda tympani into the lingual nerve, which is the branch of the Vth nerve supplying the anterior part of the tongue.

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torius. Above this the narrow taeniae from the two sides come together so as to form a thin triangular sheet, the *ober*. The taeniae continue to the under surface of the cerebellum as the *posterior medullary velum*. The rostral part of the rhomboid fossa is covered by the cerebellum and the *anterior medullary*

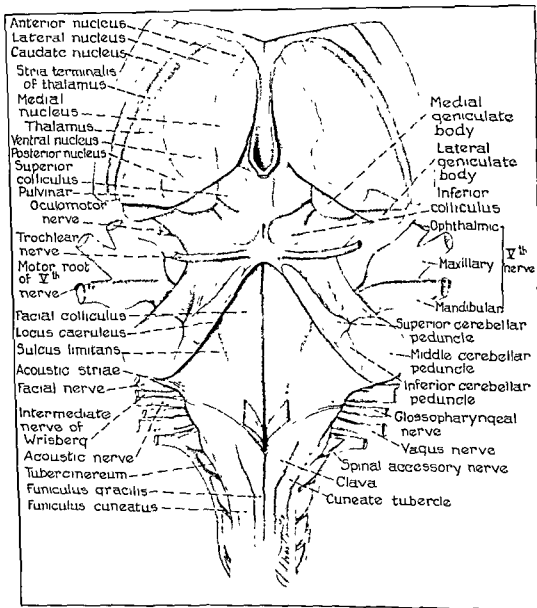


FIG. 83.—DORSAL VIEW OF BRAIN STEM, INCLUDING MEDULLA OBLONGATA.

velum At the lower end of the ventricle and at the extremities of the lateral recesses there are small openings through the tela chorioidea which allow escape of cerebrospinal fluid from the fourth ventricle into the subarachnoid space. The lower opening is called the *foramen of Magendie*. Those at the tips of the lateral recesses are known as the *foramina of Luschka*. They are also sometimes known as the *foramina of Kcy and Retzius*.

The *posterior intermediate sulcus* lies lateral to the clava and the continuation of the latter into the *funiculus gracilis*. It separates the clava from the *tuberculum cuneatum* or *nucleus of fasciculus cuneatus* and its caudal continuation, the *funiculus cuneatus*.

The *posterior lateral sulcus* forms the lateral boundary of the *funiculus cuneatus* and its nucleus, separating them from the *tuberculum cinereum*, which is formed chiefly by the *spinal Vth tract and nucleus*. The roots of the IXth, Xth and XIth nerves emerge from this sulcus. Both afferent and efferent fibers

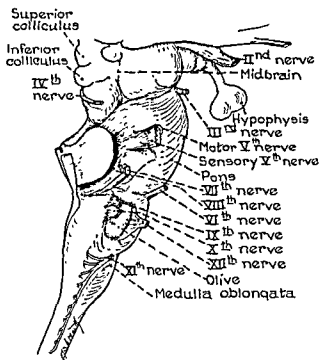


FIG 82.—LATRAL VIEW OF MEDULLA OBLONGATA.

are included in the IXth and Xth roots. Only efferent fibers are present in the XIth roots.

The upper part of the medulla oblongata is flattened and expanded. The floor of the fourth ventricle, known as the *rhomboid fossa*, extends laterally behind the inferior cerebellar peduncles, forming a *lateral recess* on each side. The floor of the ventricle has a number of markings formed by the deeply placed nuclei and other structures. The lateral walls, save at the tips of the lateral recesses, are formed of massive nervous tissue. The margin of the ventricle is formed by a band-like *taenia*, to the edge of which is attached a sheet of ependymal epithelium which forms the innermost layer of the ventricular roof. External to the epithelial layer there is a layer of pia mater called the *tela chorioidea*. It contains numerous blood vessels forming the *chorioid plexus* of the fourth ventricle.

The lower end of the ventricle tapers to a point, called the *calamus script-*

The visceral efferent fibers emerge from the visceral efferent column and the somatic efferent fibers of the XIIth nerve emerge from the somatic efferent column. The latter have a more ventral zone of emergence than do the visceral motor fibers.

While the four columns named can be recognized in man, the relative simplicity of arrangement is lost. This is due to the entrance of numerous special fibers and to the fact that the bundles ascending from the cord become rearranged, either by interposition of nuclei in their course, e.g., the fibers of the dorsal funiculus, or by enlargement of various masses of bulbar gray matter

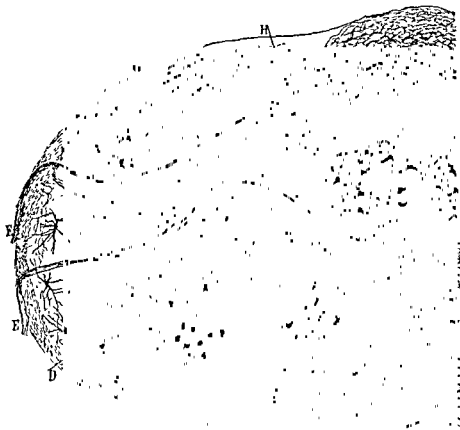


FIG 85—CROSS SECTION OF MEDULLA OBLONGATA OF MOUSE. GOLGI METHOD (From Cajal.)

A, hypoglossal nucleus, *B*, commissural ganglion; *C*, olivary nucleus, *D*, spinal Vth tract, *E*, motor roots of IXth and Xth nerves; *F*, nucleus ambiguus; *G*, terminal portion of the vestibular spinal nucleus; *H*, transverse section of the solitary tract; *L*, fibers to olivary nucleus; *a*, pyramids, *b*, collaterals from fibers of and near pyramids; *c*, raphe; *d*, collaterals from lateral column; *e*, sensory collaterals to nucleus ambiguus; *f*, recurrent fibers of motor root passing to spinal Vth tract; *j*, crossed motor roots of IXth and Xth nerves, *h*, collaterals of sensory root of these nerves to nucleus of solitary tract.

which displace the spinal tracts. In addition to the four general functional columns named, corresponding to those of the cord, there are present in the bulb several special columns, namely, *special somatic afferent*, *special visceral efferent* and *special somatic efferent*.

In the human medulla oblongata the columns of gray substance as well as the

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In lower vertebrates the floor of the ventricle is marked by four longitudinal columns which represent nuclei of gray matter. The most medial on each side of the midline is the somatic motor column. It lies in the same relative position as the ventral gray column of the cord. Lateral to it lies the visceral motor

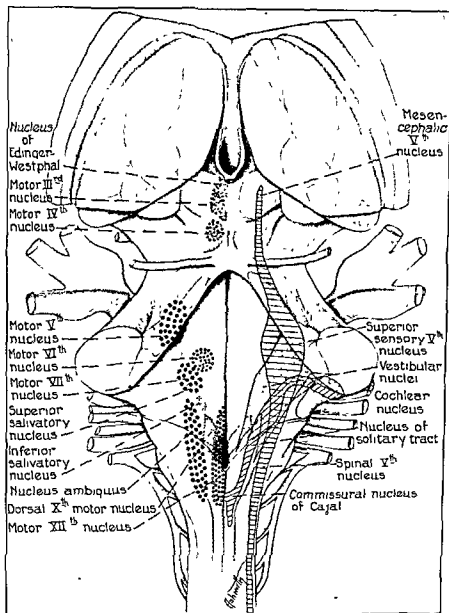


FIG. 84.—MOTOR AND SENSORY NUCLEI OF MEDULLA OBLONGATA.

In part from Herrick.

column, corresponding in position, in general, to the intermediolateral column of the cord. A prominent furrow, the *sulcus limitans*, recognizable in man (Fig. 83), bounds this column laterally and thus separates the visceral motor column from the visceral sensory column which lies lateral to the sulcus. At the dorso-lateral margin of the rhomboid fossa is found the somatic sensory column

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modifies the pattern of internal arrangement, as it courses upward on each side of the median plane.

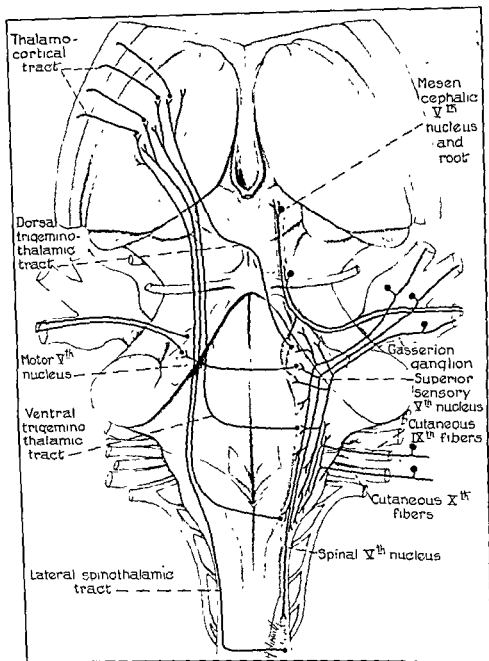


FIG. 87.—DIAGRAM OF CUTANEOUS AND SOME REFLEX CONNECTIONS OF MEDULLA OBLONGATA.

MOTOR NUCLEI

VENTRAL NUCLEUS OF THE SPINAL ACCESSORY NERVE—At the lower limit of the decussation of the pyramids the anterior gray column is smaller than in the upper cervical cord, with which it is continuous. It is partly separated from the remaining gray substance by bands of decussating pyramidal fibers. At the

funiculi of white substance undergo considerable rearrangement. The change is gradual in the lower part of the bulb, but is very marked above the inferior level of the olives. The deeply buried central canal of the spinal cord and lower end of the medulla oblongata gradually emerges toward the dorsal surface and expands into the fourth ventricle. The central gray substance around the canal spreads out with the ventricle into the gray substance of the ventricular floor. The remaining gray substance increases in volume and is differentiated into motor and sensory nuclei. The four functional columns above named can be recognized in man by the grouping of nuclei of the same functional types. In place of con-

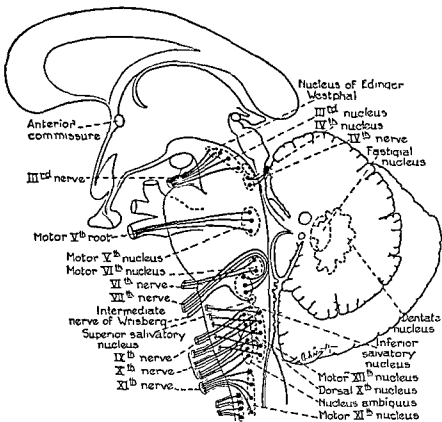


FIG. 86.—DIAGRAM OF MOTOR NUCLEI OF MEDULLA OBLONGATA AND MOTOR ROOTS OF CRANIAL NERVES.

tinuous columns of cells, however, there are distinct nuclear masses, separated by fiber masses and reticular substance.

Other changes in the medulla oblongata, as compared with the spinal cord, are due to the presence of large bundles of fibers such as the *pyramids* and the *medial lemniscus*. The pyramids descend from higher levels of the brain, covering the anterior surface of the medulla oblongata in their course to the spinal cord. The rearrangement of their fibers at the *decussation of the pyramids*, in the lower end of the medulla oblongata, brings about much modification in the latter from the simple pattern of structure found in the spinal cord. The medial lemniscus has its origin in the lower part of the medulla oblongata and further

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cervical cord, but also disappears at the lower level of the decussation of the medial lemniscus.

NUCLEUS FASCICULUS GRACILIS AND NUCLEUS FASCICULUS CUNEATUS (DORSAL NUCLEI).—The central gray substance increases in mass and assumes a quadrilateral form, in cross section, in the lower part of the medulla oblongata. At the upper levels of the decussation of the pyramids it shows the beginning of dorsal extensions which represent the *nucleus gracilis* and the *nucleus cuneatus*. These are new features in the gray substance. They are the terminal nuclei of the fasciculus gracilis and of the fasciculus cuneatus, respectively. Their large masses of cells give rise to elevations on the surface of the medulla oblongata known as the *clava*, above the gracile nucleus, and the *cuneate tubercle* above the cuneate nucleus.

These nuclei extend forward to about the middle level of the inferior olives,

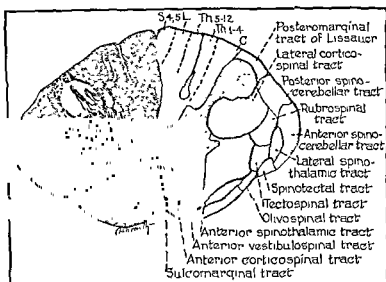


FIG. 89.—CROSS SECTION OF SPINAL CORD JUST BELOW DECUSSATION OF PYRAMIDS.

giving off fibers which form important additions to the *internal arcuate fibers* of the medulla oblongata. Most of the internal arcuate fibers from the dorsal nuclei decussate and turn rostrally as the medial lemniscus. Others are described as reaching the cerebellum through the restiform body. *Dorsal external arcuate fibers* from the dorsal nuclei pass into the restiform body of the same side to reach the cerebellum.

SOMATIC MOTOR NUCLEI.—The ventral spinal accessory nucleus has already been named. Above the decussation of the pyramids the central gray substance enlarges ventrally to form the *nucleus of the XIIth nerve*, the motor nerve of the tongue. This is an elongated group of cells extending to the acoustic striae, rostrally, and forming a triangular eminence in the floor of the fourth ventricle known as the *trigonum hypoglossi*. The fibers from this nucleus emerge as a series of rootlets between the inferior olive and the pyramids. The *nucleus of the VIth nerve (abducens nucleus)* lies near the midplane in the same longi-

middle level of the decussation it is quite small and is completely cut off from the central gray mass by intervening pyramidal fibers. It disappears, save for a few cells, at the level of the decussation of the medial lemniscus. In this way the ventral nucleus of the spinal accessory nerve becomes a distinct mass at its upper

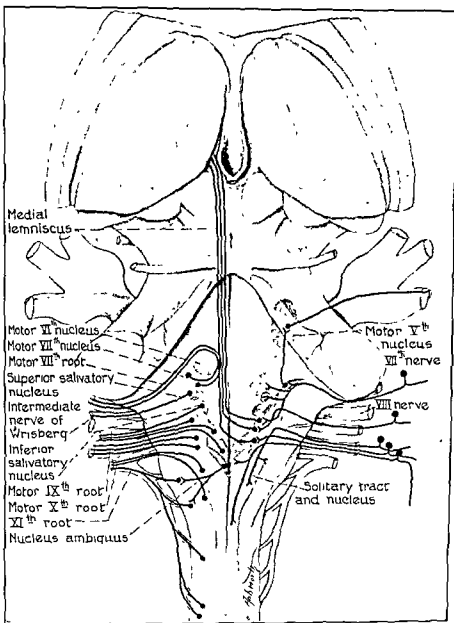


FIG 88.—VISCERAL AFFERENT AND VISCERAL EFFERENT NUCLEI AND CRANIAL NERVE ROOTS.

end while continuous with the anterior column of the spinal cord below. The lower portion gives rise to motor fibers of the 1st cervical nerve. The nucleus is augmented by the ventral portion of the lateral gray column. This increases in size at the lower level of the pyramidal decussation, as compared with the

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to migrate during ontogenetic as well as phylogenetic development toward the source of their chief stimuli.

The *motor Vth nucleus* lies in line with the VIIth nucleus and the nucleus ambiguus in the upper levels of the tegmentum of the pons. It gives origin to the fibers of the motor Vth nerve supplying the muscles of mastication.

SENSORY NUCLEI

SOLITARY TRACT AND NUCLEUS—Since, as described in the chapter on the cranial nerves, the VIIth, IXth and Xth nerves possess the same five functional components, part of the medulla oblongata shows a pattern of organization not unlike the spinal cord. The visceral afferent fibers, as they enter from the three nerves, become arranged into a distinct bundle known as the *solitary tract* (Fig. 88). This runs from the lower end of the medulla oblongata, where it exchanges fibers through the *commissure of Cajal* with the corresponding tract of the

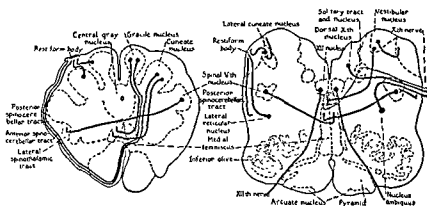


FIG 91—DIAGRAM OF SOME CONNECTIONS IN THE MEDULLA OBLONGATA AT THE LEVEL OF THE PYRAMIDS.

other side, to the level of the entering fibers of the VIIth nerve. It is parallel to the main nuclear mass of the visceral sensory column, known as the *nucleus of the solitary tract*, lying ventral and ventrolateral to it. The visceral afferent fibers eventually terminate in this nucleus to form reflex connections and relays to higher centers.

In like manner the somatic afferent fibers (Fig. 87) from the Vth, VIIth, IXth and Xth nerves are regarded as entering a common tract. This is called the *spinal Vth tract* because the majority of its fibers are derived from the chief cutaneous sensory nerve of the head, namely, the trigeminus. In lower vertebrates it is clear that cutaneous fibers from all of the nerves named enter this tract.

The **NUCLEUS OF THE SPINAL VTH TRACT** (Figs. 84 and 98) lies parallel to, and receives terminal fibers from, the spinal Vth tract. This nucleus is continuous with the *gelatinous substance* of Rolando of the cord, which receives terminals of cutaneous fibers of the spinal nerves corresponding to those of the

tudinal column as the hypoglossal nucleus. It is separated from the latter by transverse fiber masses so that it forms a distinct nuclear mass.

GENERAL VISCERAL MOTOR NUCLEI.—The *dorsal Xth nucleus*, giving rise to the general visceral motor fibers of the IXth and Xth nerves, is the principal general visceral motor nucleus. It is located below the *ala cinerea*, lateral to the hypoglossal nucleus. Rostral and somewhat lateral to the dorsal Xth nucleus are found the *inferior* and *superior salivatory nuclei*. The inferior nucleus supplies motor fibers to the parotid gland through the IXth nerve and otic ganglion. The superior nucleus supplies secretory fibers to the submaxillary and sublingual

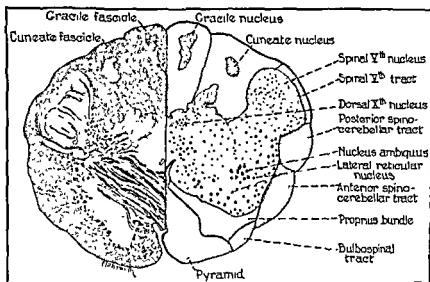


FIG. 90.—CROSS SECTION OF MEDULLA OBLONGATA AT LEVEL OF DECUSATION OF PYRAMIDS.

glands through the intermediate nerve of Wrisberg, chorda tympani and submaxillary ganglion.

SPECIAL VISCERAL MOTOR NUCLEI.—The *nucleus ambiguus* or *ventral Xth nucleus* lies in the lateral part of the reticular formation between the inferior olivary nucleus and the rootlets of the IXth and Xth nerves. It is an elongated mass of cells, extending from the level of the calamus scriptorius to the acoustic striae. It tapers somewhat caudally. Its cells give rise to motor fibers of the IXth and Xth nerves, supplying the striated muscles of the larynx, pharynx and palate, i.e., branchiomeric muscles.

The *VIIth motor* or *facial nucleus* lies in the ventrolateral part of the reticular formation above the nucleus ambiguus but in line with it. The cells give rise to fibers forming a large bundle which passes dorsomedially to the medial side of the VIth nucleus and then hooks over the latter to emerge just behind the pons. The facial nucleus gives rise to motor fibers to the muscles of expression. The relation of this nucleus and its fibers to the VIth nucleus is a classic example of Kappers' law of neurobiotaxis, according to which nuclear masses tend

to migrate during ontogenetic as well as phylogenetic development toward the source of their chief stimuli.

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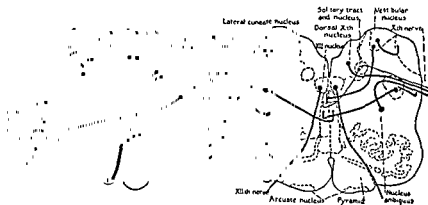


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THE NUCLEUS OF THE SPINAL VTH TRACT (Figs. 84 and 98) lies parallel to, and receives terminal fibers from, the spinal Vth tract. This nucleus is continuous with the gelatinous substance of Rolando of the cord, which receives terminals of cutaneous fibers of the spinal nerves corresponding to those of the

trigeminal from the skin of the head. The central fibers of the trigeminal differ from those of the cord by the fact that the ascending rami are short while the descending rami are long. This appears true also of the cutaneous fibers of VIIth, IXth and Xth.

SPECIAL SOMATIC AFFERENT AREA.—The dorsolateral margin of the medulla oblongata is entered by the VIIIth nerve. Two special cell masses, the *dorsal* and the *ventral cochlear nuclei* (Fig. 127) receive the cochlear fibers directly. They lie at the dorsolateral margin of the medulla oblongata. Medial to the cochlear nuclei and extending rostrally and caudally from them are the *vestibular nuclei*, four in number, which receive terminal fibers of the ves-

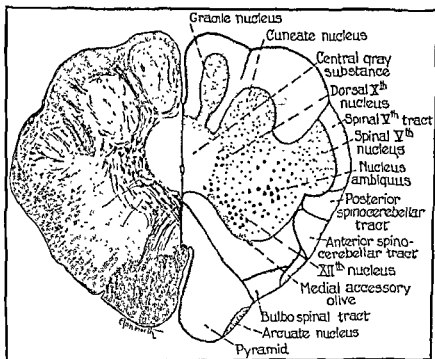


FIG. 92.—CROSS SECTION OF MEDULLA OBLONGATA AT LEVEL OF DORSAL NUCLEI.

tibular division of the VIIIth nerve. The four vestibular nuclei are the *superior* or *Bechterew's nucleus*, the *medial* or *Schwalbe's nucleus*, the *lateral* or *Deiters' nucleus*, and the *spinal vestibular nucleus*.

In fishes and salamanders the special somatic afferent column extends caudally, as the *acousticolateral area*, to the lower level of the Xth roots, receiving lateral-line, vestibular and such acoustic fibers as are present. In the transition from water to land habitat the lateral-line system is lost, but a remarkable adaptation of the acousticolateral area is effected which transforms it into purely vestibular and acoustic nuclei. This is shown in the metamorphosis of the frog tadpole, as well as in the contrast between salamanders and the adult frog.

THE MEDULLA OBLONGATA

LEMNISCUS SYSTEMS

The *medial lemniscus* is one of the most important features of the medulla oblongata. As already stated it has its origin from the dorsal nuclei. It begins just above the rostral level of the decussation of the pyramids. The fibers cross the midplane as internal arcuate fibers forming the *decussation of the medial lemniscus* and then ascend to the thalamus. The decussation extends rostrally to about the middle of the inferior olives. At this level the nuclei of the fasciculus

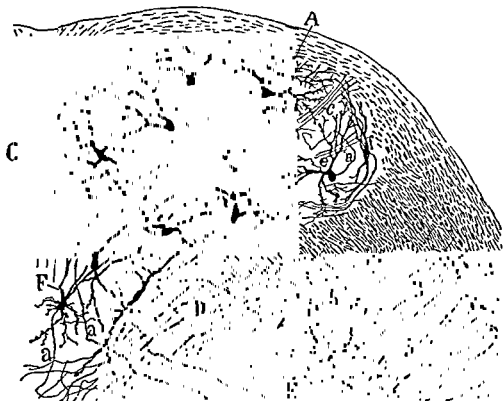


FIG 93—SECTION OF MEDULLA OBLONGATA OF KITTEN AT LEVEL OF DORSAL NUCLEI GOLGI METHOD (From Cajal)

A, nucleus of the fasciculus cuneatus, *B*, gelatinous substance of Rolando; *C*, nucleus of the fasciculus gracilis; *D*, collaterals; *E*, boundary of lateral column; *F*, peduncle of nucleus of fasciculus gracilis; *a*, axons; *b*, bundles of ascending sensory roots

gracilis and fasciculus cuneatus end, and internal arcuate fibers from this source cease to be given off

The medial lemniscus, however, is augmented by fibers from the sensory nuclei of the cranial nerves lying more rostrally in the medulla oblongata so that it becomes the principal sensory pathway through the brain stem as far as the thalamus. In the lower part of its course it has a vertical position, in transverse sections, on each side of the median raphé. Dorsal to the pons, however, it gradually assumes a horizontal and more lateral position as if twisted sideways and continues so into the midbrain. The change in position is due in part to

trigeminal from the skin of the head. The central fibers of the trigeminal differ from those of the cord by the fact that the ascending rami are short while the descending rami are long. This appears true also of the cutaneous fibers of VIIth, IXth and Xth.

SPECIAL SOMATIC AFFERENT AREA.—The dorsolateral margin of the medulla oblongata is entered by the VIIIth nerve. Two special cell masses, the *dorsal* and the *ventral cochlear nuclei* (Fig. 127) receive the cochlear fibers directly. They lie at the dorsolateral margin of the medulla oblongata. Medial to the cochlear nuclei and extending rostrally and caudally from them are the *vestibular nuclei*, four in number, which receive terminal fibers of the ves-

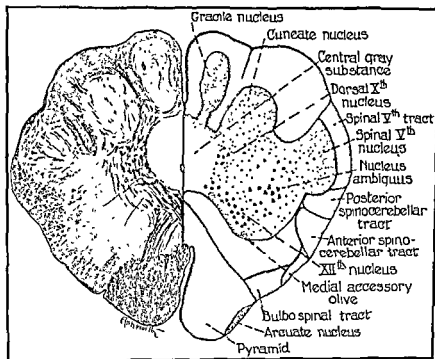


FIG. 92.—CROSS SECTION OF MEDULLA OBLONGATA AT LEVEL OF DORSAL NUCLEI.

tibular division of the VIIIth nerve. The four vestibular nuclei are the *superior* or *Bechterew's nucleus*, the *medial* or *Schwalbe's nucleus*, the *lateral* or *Deiters' nucleus*, and the *spinal vestibular nucleus*.

In fishes and salamanders the special somatic afferent column extends caudally, as the *acusticolateral area*, to the lower level of the Xth roots, receiving lateral-line, vestibular and such acoustic fibers as are present. In the transition from water to land habitat the lateral-line system is lost, but a remarkable adaptation of the acusticolateral area is effected which transforms it into purely vestibular and acoustic nuclei. This is shown in the metamorphosis of the frog tadpole, as well as in the contrast between salamanders and the adult frog.

THE MEDULLA OBLONGATA

The *dorsal secondary Vth tract*. Touch fibers from the face appear to end chiefly in the superior sensory Vth nucleus. These include light touch as well as fibers carrying discriminative impulses. There is little dissociation of these differences of sensation in the medulla oblongata corresponding to that in the spinal cord. The superior sensory Vth nucleus gives rise to the dorsal secondary Vth tract, which reaches the lateral nucleus of the thalamus with the ventral secondary Vth tract. The two groups of secondary Vth fibers constitute the *trigeminal lemniscus*.

OTHER STRUCTURES

The *INFERIOR OLIVE* (Figs. 95 and 96) is a rounded projection on the surface of the medulla oblongata produced by the *inferior olivary nuclei*. In addition to

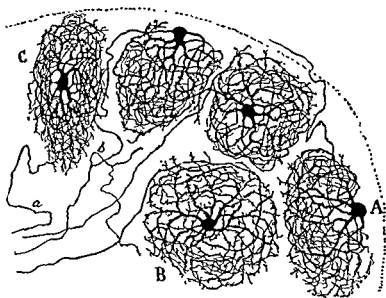


FIG 95—CELLS OF THE INFERIOR OLIVE OF NEW BORN CHILD (From Cajal.)
A, marginal cell, B, deep cell, a, axon, b, collateral.

the main nucleus there is a *dorsal accessory* and a *medial accessory olivary nucleus*. The main nucleus consists of a much folded layer of gray matter containing numerous rather small cells. These give rise to fibers which emerge from the capsule of the nucleus at the medially placed hilum to form the *peduncle of the olive*. The emerging fibers form the *olivocerebellar tract*, reaching the cerebellum on the opposite side after decussating in the midplane and ascending through the restiform body.

A small nuclear mass, the *arcuate nucleus*, lies among the ventral arcuate fibers between the pyramid and the surface. In their course through the medulla oblongata, after decussation, they form part of the system of *internal arcuate fibers*. The olivary internal arcuate fibers are smaller than those of the medial lemniscus. In addition to cerebellar connections from the olivary nucleus, there are claims of cerebello-olivary connections, but their existence is not established.

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additions from nuclei in the upper part of the medulla oblongata to the main mass of fibers derived from the dorsal nuclei.

A large mass of fibers from the nuclei related to the cochlear apparatus forms the *lateral lemniscus*, which takes its course lateral and parallel to the medial lemniscus as far as the inferior colliculus. The lateral lemniscus terminates in the inferior colliculus and the medial geniculate body.

The *spinal lemniscus*, consisting of spinotectal and spinothalamic tracts, ventral and lateral, takes its course in the lower part of the medulla oblongata as a separate bundle. It lies dorsolateral to the inferior olivary nucleus and lateral to the reticular formation. It gradually becomes included in the general mass

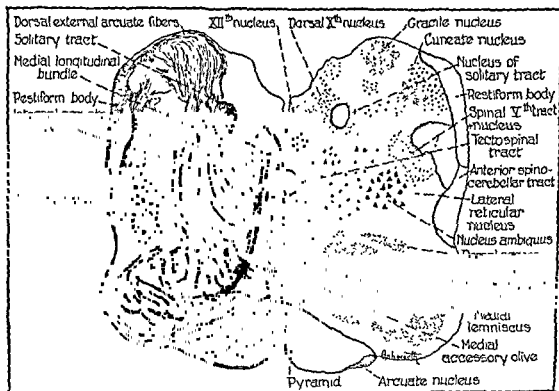


FIG. 94.—CROSS SECTION OF MEDULLA OBLONGATA AT LOWER LEVEL OF INFERIOR OLIVE.

of the medial lemniscus, adding fibers conveying impulses of pain and temperature from the spinal cord. Fibers of light touch and tactile discrimination are found in the dorsal part of the medial lemniscus throughout its length. Such fibers are derived from the dorsal nuclei.

The *ventral secondary trigeminal tract*, derived from the spinal Vth nucleus and carrying principally pain and temperature impulses from the face and head, also is gradually incorporated into the medial lemniscus. This tract is formed of somewhat scattered fibers in the lower part of the medulla oblongata, only some ascending with the medial lemniscus. In the pons region they have become a part of the general lemniscus mass, lying medial to the lateral lemniscus.

stices between the interlacing bundles are occupied by nerve cells, some aggregated into small nuclear masses. Longitudinal fiber bundles run through the reticular formation. The largest of these is the *medial lemniscus*, which lies close to the midplane dorsal to the pyramid. It receives internal arcuate fibers from the bulbar nuclei, forming the main bundle between them and the thalamus. Above the medial lemniscus is found the continuation from the cord of the *ventral spinothalamic tract*, and above this in turn lies the *tectospinal tract*. The *median longitudinal bundle* lies above the latter.

The **INFERIOR CEREBELLAR PEDUNCLE** OR **RESTIFORM BODY** is a thick mass of fibers lateral to the lower part of the fourth ventricle, which connects the medulla oblongata and spinal cord with the cerebellum. It contains the continuation of the *dorsal spinocerebellar tract*, *direct vestibular fibers*, *nucleovestibular fibers*, *olivocerebellar fibers*, fibers from *arcuate and lateral reticular nuclei*, *posterior external arcuate fibers* from the external cuneate nucleus and perhaps from the nucleus gracilis of the same side. Descending fibers from the cerebellum are found in the inferior peduncle, as described in the chapter on the cerebellum.

CLINICAL INTERPRETATION

SOME LESIONS OF THE MEDULLA OBLONGATA AND PONS

In lesions of the medulla oblongata there are various combinations of motor and sensory phenomena not met with in lesions of the spinal cord. These are due to the rearrangement of fiber tracts, the crossing of important motor and sensory pathways, and the individual nuclei of several of the cranial nerves connected with the medulla oblongata. Circumscribed lesions may affect motor and sensory fibers alone or such fibers in combination with bulbar nuclei in a great variety of patterns.

A lesion in the upper part of the pons may involve sensory fibers of the Vth

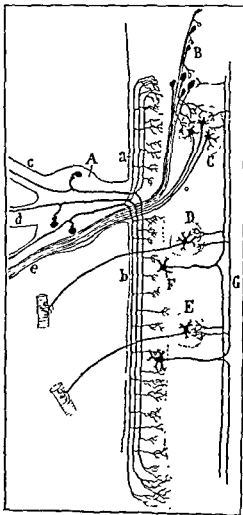


FIG. 98—CONNECTIONS OF THE VTH NERVE. (From Cajal)

A, gasserian ganglion; B, mesencephalic Vth nucleus; C, motor Vth nucleus; D, motor Vth nucleus; E, hypoglossal (XIIth) nucleus; F, cells of spinal Vth nucleus; G, secondary sensory Vth tract; a, ascending branch of sensory root; b, descending branch; c, ophthalmic division; d, maxillary division; e, mandibular division.

There are also indications of homolateral cerebro-olivary connections. Collateral branches of the corticospinal tract enter the inferior olivary nucleus. There are also fibers from the reticular formation.

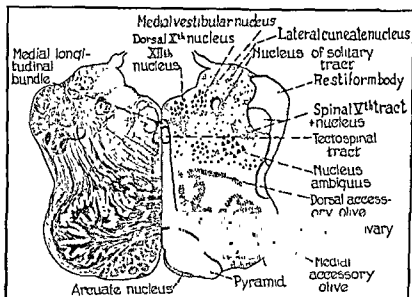


FIG. 96.—CROSS SECTION OF MEDULLA OBLONGATA AT MIDDLE LEVEL OF INFERIOR OLIVE.

The RETICULAR FORMATION of the medulla oblongata is a mass of nerve fibers and cells extending from below the floor of the fourth ventricle to the

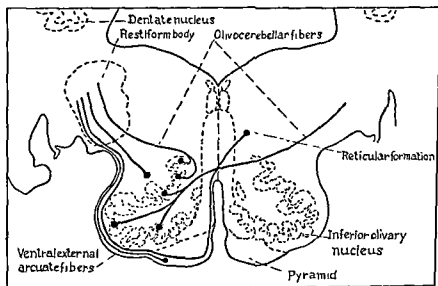


FIG. 97.—DIAGRAM OF SOME CONNECTIONS OF INFERIOR OLIVE AND OF VENTRAL EXTERNAL ARCUATE FIBERS.

pyramids and olivary nucleus, and from the midplane to the inferior cerebellar peduncle, laterally. The fiber bundles run at various angles to each other, some being directed longitudinally and others transversely or nearly so. The inter-

nerve and also the medial lemniscus. In such a case there would be sensory paralysis of the face on the side of the lesion, and loss of sensation in the body and limbs on the opposite side.

SYNDROME OF AVELLIS.—A lesion may be so circumscribed as to involve only the nucleus ambiguus and the spinal lemniscus. This results in loss of pain and temperature sensation from the neck down, on the opposite side of the body, together with paralysis of the vocal cords and half of the palate on the side of the lesion. The sensory loss on the opposite side of the body is due to involvement of the lateral spinothalamic tract which has already crossed in the spinal cord. The motor loss is due to lower motor injury of vagus fibers to the muscles of the palate and the vocal cords which arise from the nucleus ambiguus.

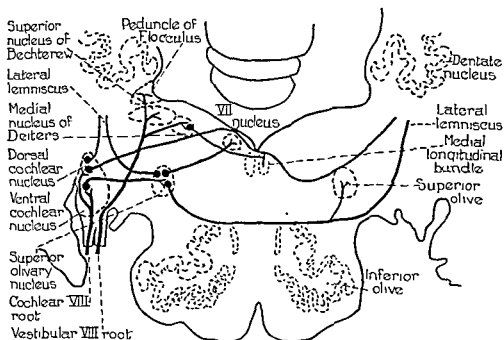


FIG 100—DIAGRAM OF CONNECTIONS OF ACOUSTIC NERVE.

Alternate paralysis of the extremities (crossed hemiplegia), involving one arm and the opposite leg, may be brought about by lesions in the medulla oblongata if located between the decussation of fibers to the upper extremities and those to the lower extremities. The former cross at a higher level than do the latter. The lesion must therefore be located on the side represented by the upper extremity paralysis and opposite to that of the lower extremity paralysis. The paralysis in both cases is of the spastic type, since upper motor neurons are involved.

SYNDROME OF MILLARD-GÜBLER.—A lesion involving the roots of the VIth nerve and the pyramid on one side results in paralysis of the external rectus muscle on the same side, with motor paralysis of the opposite half of the body (hemiplegia). The external rectus paralysis results in internal squint of the

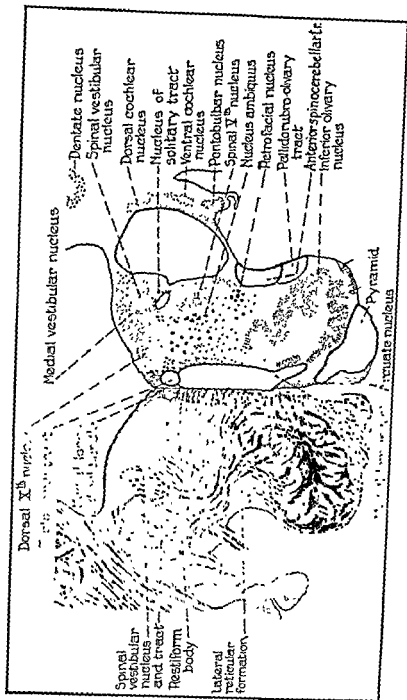


FIG. 99.—CROSS SECTION OF MEDULLA OBLONGATA AT LEVEL OF EIGHTH NERVE.

THE MEDULLA OBLONGATA

nerve and also the medial lemniscus. In such a case there would be sensory paralysis of the face on the side of the lesion, and loss of sensation in the body and limbs on the opposite side.

SYNDROME OF AVELLIS.—A lesion may be so circumscribed as to involve only the nucleus ambiguus and the spinal lemniscus. This results in loss of pain and temperature sensation from the neck down, on the opposite side of the body, together with paralysis of the vocal cords and half of the palate on the side of the lesion. The sensory loss on the opposite side of the body is due to involvement of the lateral spinothalamic tract which has already crossed in the spinal cord. The motor loss is due to lower motor injury of vagus fibers to the muscles of the palate and the vocal cords which arise from the nucleus ambiguus.

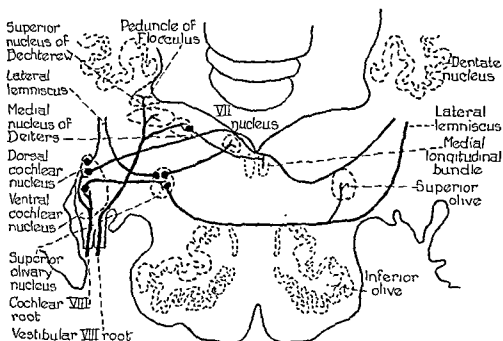


FIG 100.—DIAGRAM OF CONNECTIONS OF ACOUSTIC NERVE.

Alternate paralysis of the extremities (crossed hemiplegia), involving one arm and the opposite leg, may be brought about by lesions in the medulla oblongata if located between the decussation of fibers to the upper extremities and those to the lower extremities. The former cross at a higher level than do the latter. The lesion must therefore be located on the side represented by the upper extremity paralysis and opposite to that of the lower extremity paralysis. The paralysis in both cases is of the spastic type, since upper motor neurons are involved.

SYNDROME OF MILLARD-GÜBLER.—A lesion involving the roots of the Vth nerve and the pyramid on one side results in paralysis of the *external rectus* muscle on the same side, with motor paralysis of the opposite half of the body (hemiplegia). The external rectus paralysis results in internal squint of the



FIG. 101.—CROSS SECTION AT LEVEL OF PONS AND SENSORY NUCLEI OF VTH NERVE.

THE MEDULLA OBLONGATA

affected eye and double vision. The lower motor neuron is involved in the eye muscle paralysis, and the upper motor neuron, above the decussation of the pyramids, is involved in the body and limb muscle paralysis. The latter is therefore of the spastic type.

Alternating hypoglossal and one sided paralysis (syndrome of the pyramidal tract and hypoglossal nerve), is produced by lesions involving the pyramid and the roots of the XIIth nerve on the same side. Injury to the latter results in flaccid paralysis with atrophy of the tongue musculature on the affected side, giving the tongue a corrugated surface. When protruded the tip of the tongue will turn toward the affected side. The injury to the pyramidal tract above the decussation of the pyramids results in spastic paralysis of the arm and leg on the opposite side, accompanied by the Babinski reflex, ankle clonus and exaggerated tendon reflexes such as the knee-jerk.

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CHAPTER 10

THE VISCERAL SYSTEM

The visceral system of nerves and ganglia, usually called the sympathetic system, is concerned with regulation of the internal organs, the blood vessels, and the glands of the body. It is part of the peripheral nervous system and is connected with many of the cerebrospinal nerves and through them, with the brain and cord (Fig. 102). As in the somatic system there are afferent and efferent fibers.

The VISCERAL AFFERENT SYSTEM is scattered, fibers being found in several of the cranial nerves and in nerves leading to the thoracic and abdominal viscera. These lead to receptors located in mucous membranes and in the walls or capsules of visceral organs. The fibers reach the brain or spinal cord through spinal and cranial nerves, in whose sensory ganglia their nerve cells are located. They form the afferent links of visceral reflex arcs which are concerned, in general, with regulation of the activity of smooth muscle and glands. Aside from the *special visceral afferent* stimuli of taste and smell, visceral afferent impulses rarely reach the conscious level, although they play a rôle in producing so-called referred pain.

The VISCERAL EFFERENT SYSTEM is called the *autonomic system*, a term introduced by Langley. It is subdivided, according to the location of its central cells and the nerves which distribute its fibers, into *cranial*, *thoracolumbar* and *sacral* divisions. The cranial and the sacral divisions have in common the fact that their ganglia lie in or near the organs they innervate. They also have certain physiological and pharmacological characteristics in common, which contrast these divisions with the thoracolumbar division. Together they are usually spoken of as the *craniosacral autonomic system*, or the *parasympathetic system*. The nerve fibers from brain and cord, called the *preganglionic fibers* (Fig. 103), approach the peripheral ganglia through the IIIrd, VIIth, IXth, Xth, and XIth cranial nerves, and through the *nervus erigens* (*pelvic nerve*), made up of fibers from the 2nd, 3rd, and 4th sacral nerves. All of these nerves have other functional components and the fibers in question constitute only the visceral efferent component. Histologically they may be recognized as small, myelinated fibers, 1.5 to 4 microns in diameter. On reaching the peripheral ganglia the fibers branch and make synaptic connections with ganglionic nerve cells. This is usually accomplished by synaptic networks about the cell bodies.

The axons of the ganglion cells extend from the ganglion to the organ

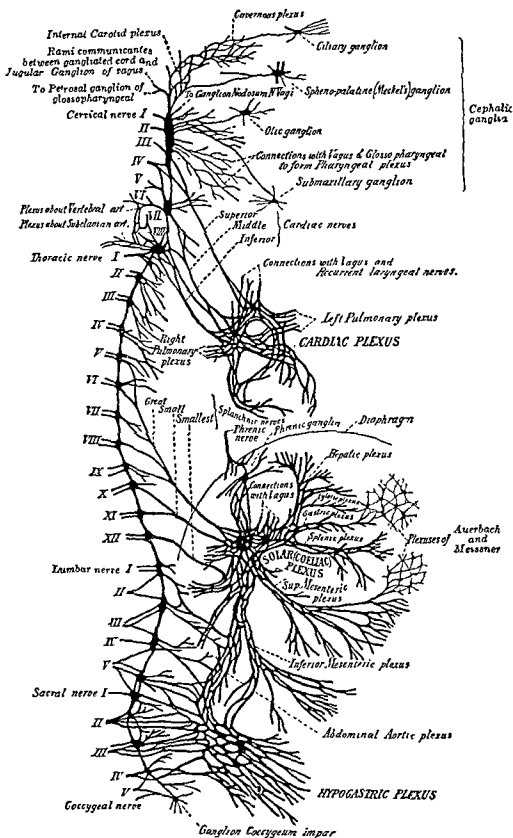


FIG 102—THE SYMPATHETIC SYSTEM

From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co, 1933.

CHAPTER 10

THE VISCERAL SYSTEM

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The axons of the ganglion cells extend from the ganglion to the organ

THORACOLUMBAR DIVISION

The THORACOLUMBAR VISCERAL EFFERENT OF AUTONOMIC division (Fig. 104) consists of a paired trunk of nerve fibers and ganglia extending from the superior cervical ganglion in the upper part of the neck, to the ganglion impar, anterior to the 5th sacral vertebra. In addition to the ganglia of the trunk, called because of their position with relation to the vertebrae the *prevertebral*

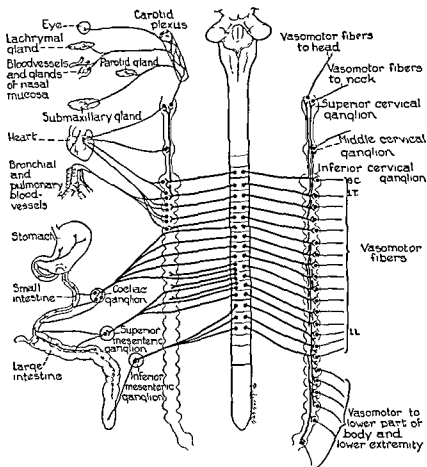


FIG. 104—SCHEMA OF THORACOLUMBAR VISCERAL EFFERENT CONNECTIONS, SHOWING THOSE TO INTERNAL VISCERA ON LEFT SIDE AND THOSE TO PERIPHERY ON RIGHT SIDE

ganglia, there are *collateral ganglia*, such as the coeliac, which, with their fibers of distribution, constitute a part of this division. There are also three cervical ganglia, the superior, middle and inferior, in the cervical part of the sympathetic trunk.

The preganglionic fibers of the thoracolumbar division have their origin from cells of the intermediolateral column of gray matter of the 8th cervical or 1st thoracic to the 2nd to 4th lumbar segments of the spinal cord. They leave the cord with the ventral root fibers of the corresponding segmental nerves,

innervated and end in relation to smooth muscle or gland cells. Such processes are called *postganglionic fibers* (Fig. 103). In the craniosacral divisions of the visceral efferent system the postganglionic fibers are relatively short. It will be noted that there are two neurons in the visceral motor apparatus. One, giving rise to the preganglionic fiber, is located in the visceral motor nuclei of the brain stem or in the intermediolateral gray column of the cord. The second in the chain is located in the peripheral ganglion and gives off the postganglionic

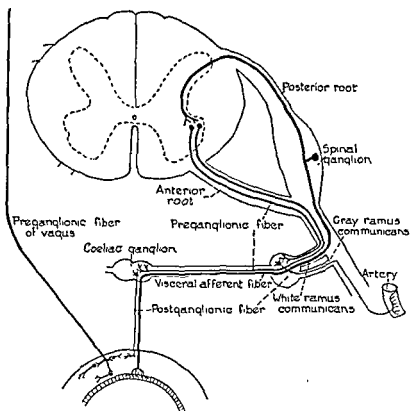


FIG 103.—DIAGRAM OF PRE- AND POST-GANGLIONIC FIBERS AND THEIR RELATION TO CENTRAL NERVOUS SYSTEM AND PERIPHERAL GANGLIA.

fibers. Each preganglionic fiber, through its terminal branches, makes synaptic connections with many ganglion cells, thus activating a large number of effector elements. This arrangement also holds for the thoracolumbar autonomic system. Ranson and Billingsley have shown that the average is 32 cells in the superior cervical ganglion of the cat for each preganglionic fiber in the cervical sympathetic trunk above the middle cervical ganglion. By this arrangement impulses are widely diffused in the visceral efferent systems.

THE VISCERAL SYSTEM

ganglia to the spinal nerves, in addition to connections from these ganglia to visceral organs through the various plexuses.

The thoracolumbar part of the visceral efferent system serves, in general,

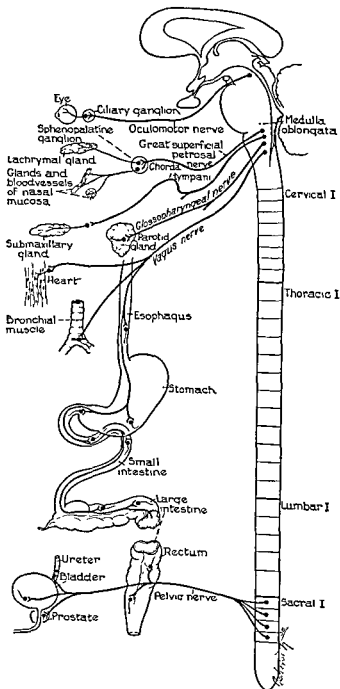


FIG 105—SCHEMA OF CRANIOSACRAL VISCERAL EFFERENT CONNECTIONS.

to diffuse motor stimuli to peripheral organs. It is so built as to accomplish this function with a minimum of central mechanism, the diffusion being accomplished through the multiple connections with cells in the sympathetic chain

becoming included in the common spinal nerve trunk for a short distance. They leave the nerve trunk through the white communicating branches, which connect nerve trunks and prevertebral ganglia, to enter these ganglia. White rami are present only between the 8th cervical or 1st thoracic and the 2nd to 4th lumbar segments. All preganglionic fibers which enter the sympathetic trunk, therefore, do so in these segments of the body.

In the cat and probably in man, the fibers which enter from the 8th cervical and upper five thoracic cord segments either terminate in the first sympathetic trunk ganglion they reach or turn upward within the sympathetic trunk to terminate in a ganglion at a higher level. A large number of preganglionic fibers from the 8th cervical and the upper two or three thoracic segments reach the superior cervical ganglion. Others of the preganglionic fibers reach the middle and inferior cervical ganglia.

From the 5th to the 9th thoracic segments preganglionic fibers entering the sympathetic trunk may ascend or descend to terminate at a higher or lower level. Many end in the first ganglion they reach. Others from these segments pass through the prevertebral ganglia, without interruption, to become the small myelinated fibers of the greater splanchnic nerve and to terminate as synaptic networks about the cells of the coeliac ganglion.

The preganglionic fibers entering the trunk below the 9th thoracic segment either terminate in the first ganglion reached or pass downward in the sympathetic trunk, save those which pass through the ganglia to form the splanchnic nerves. In the 9th and 10th segments of the thorax, fibers pass through the ganglia without interruption and form the *lesser splanchnic nerve*. This enters the coeliac plexus, after piercing the diaphragm, and terminates in the *aorticorenal ganglion*. The *lowest splanchnic nerve*, when present, arises in similar manner, either from the last thoracic sympathetic ganglion or as fibers from the lesser splanchnic nerve. These fibers end in relation to the ganglion cells of the renal plexus.

The preganglionic fibers which descend in the sympathetic trunk may extend as far as the last sacral ganglion. The indications are that the preganglionic fibers from the lower thoracic and lumbar segments extend farther into the sacral part of the trunk than do those from higher segments.

Postganglionic fibers from the prevertebral and collateral ganglia are distributed to blood vessels, visceral muscle and glands. From the prevertebral ganglia fibers reach the common spinal nerve trunks through the *gray communicating branches*. These rami are gray in color, in contrast to the white rami, because they are made up of unmyelinated postganglionic fibers. The white rami receive their color from the myelin sheaths of the preganglionic fibers.

White rami are present in only the thoracic and upper lumbar segments, but gray rami are given off from all the sympathetic chain ganglia. In the thoracic and upper lumbar segments they lie side by side with the white rami. In the cervical, lower lumbar and sacral regions gray rami alone connect the

THE VISCERAL SYSTEM

great deep petrosal nerve which passes through the Vidian canal to reach the sphenopalatine ganglia. The fibers in question traverse the ganglion without interruption, some continuing through the sphenopalatine branches of the Vth nerve, the maxillary nerve, and the zygomaticotemporal nerve to reach the lachrymal gland. Others apparently are distributed to the blood vessels of the nasal region.

5. EYE.—Other branches from the internal carotid plexus pass through the

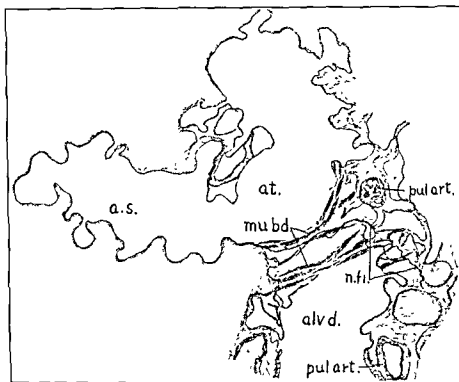


FIG 106—NERVE ENDINGS IN HUMAN BRONCHIAL MUSCLE.

alvd., alveolar duct, *as*, air sac; *at.*, atrium; *mubd*, muscle band; *n.fi*, nerve fiber; *pulart.*, pulmonary artery.

ciliary ganglion to reach the radial muscle fibers of the iris. Stimulation of these fibers causes dilatation of the pupil. It has been demonstrated that cutting only some of the long ciliary nerves is followed, on stimulation, by contraction of only part of the radial fibers of the iris, indicating that the postganglionic fibers are distributed through the several long ciliary nerves to different parts of the iris.

Some of the other chief thoracolumbar paths are summarized in Table II together with the craniosacral paths to various organs.

ganglia. The diffusion of impulses is primarily segmental, but by overlapping of preganglionic fibers into the ganglia of adjacent body segments, and even those as far removed as the cervical and the sacral, the diffusion is extended.

A typical simple example of segmental autonomic innervation is represented by the vasomotor fibers to the blood vessels of any of the thoracic segments. The preganglionic fibers arise in the intermediolateral gray column. They terminate in the prevertebral ganglion of the same segments, leading to this ganglion through the white communicating branch. They form synaptic connections with cells which give rise to postganglionic fibers. These fibers reach the peripheral common nerve trunk through the gray communicating branch, and are distributed by this nerve and its subdivisions to blood vessels and glands, chiefly of the corresponding segment. Visceral efferent fibers of segmental origin are distributed as follows:—

1. LUNGS.—The thoracolumbar autonomic fibers to the lungs arise in the upper three or four thoracic segments of the cord. The preganglionic fibers reach the stellate and inferior cervical ganglia. The postganglionic fibers pass through the pulmonary plexus to reach the blood vessels of the lung and pleura and possibly the bronchial musculature.

2. HEART.—The thoracolumbar fibers to the heart likewise arise in the upper thoracic cord. The preganglionic fibers reach the sympathetic trunk through the white rami, chiefly those to the stellate and inferior cervical ganglia. Many fibers ascend in the trunk to terminate in the superior cervical ganglion, others end in the middle cervical ganglion, and still others in the inferior cervical or stellate ganglia. Postganglionic fibers having their origin in these ganglia form respectively the superior, the middle and the inferior cardiac nerves, which pass through the cardiac plexus to terminate in the heart muscle. There are also some postganglionic fibers from the 2nd, 3rd, 4th and 5th thoracic ganglia, which reach the heart as the thoracic cardiac nerves. When the thoracolumbar autonomic nerves of the heart are stimulated the rate of the heart beat is increased. When they are cut the heart rate is retarded.

3. OTHER VISCERA.—Thoracolumbar fibers reach the remaining viscera through a series of plexuses. The pulmonary and cardiac plexuses in the thorax and the coeliac, hypogastric and pelvic plexuses of the abdominal cavity, represent the larger of the visceral plexuses. Secondary plexuses extend from them along the arteries or other organs. In addition to nerve fibers the plexuses contain clusters of ganglion cells. It is held that such ganglionic clusters receive preganglionic fibers and give off postganglionic fibers in the same manner as the coeliac ganglia in their relation to the splanchnic nerves.

4. HEAD.—Thoracolumbar fibers to the head arise from the superior cervical ganglion. Plexuses are formed on the internal and the external carotid arteries. These represent postganglionic fibers from cells in the superior cervical ganglion. They are distributed to the blood vessels of the head and to other organs, as follows: Fibers from the internal carotid plexus form part of the

THE VISCERAL SYSTEM

great deep petrosal nerve which passes through the Vidian canal to reach the sphenopalatine ganglia. The fibers in question traverse the ganglion without interruption, some continuing through the sphenopalatine branches of the Vth nerve, the maxillary nerve, and the zygomaticotemporal nerve to reach the lachrymal gland. Others apparently are distributed to the blood vessels of the nasal region

5. EYE.—Other branches from the internal carotid plexus pass through the

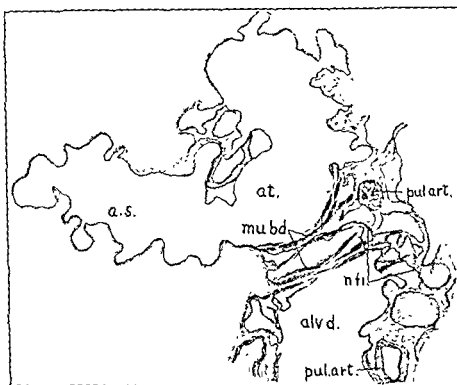


FIG 106.—NERVE ENDINGS IN HUMAN BRONCHIAL MUSCLE.

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Some of the other chief thoracolumbar paths are summarized in Table II together with the craniosacral paths to various organs.

CRANIOSACRAL DIVISION

The CRANIAL VISCERAL EFFERENT OF AUTONOMIC system (Fig. 105) is adapted for localization of visceral motor impulses, rather than their general diffusion. Instead of originating from cells of a continuous column as do the thoracolumbar fibers, the cranial autonomic preganglionic fibers are given off from relatively small circumscribed visceral motor nuclei in the brain stem. They terminate in synaptic relation to cells in the cranial sympathetic ganglia,

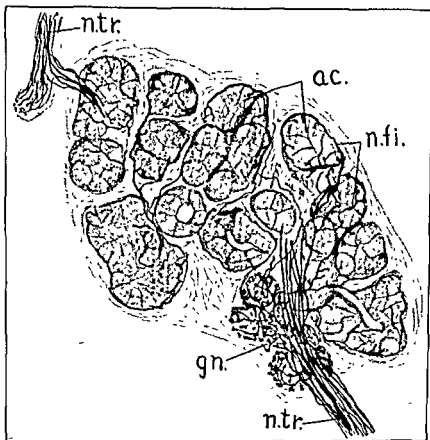


FIG. 107—NERVE ENDINGS IN HUMAN BRONCHIAL MUCOUS GLAND.

ac., acinus; *gn.*, ganglion; *n.fi.*, nerve fiber; *n.tr.*, nerve trunk.

namely, the ciliary, the sphenopalatine, the otic and submaxillary, or the cardiac, bronchopulmonary and enteric ganglia. Postganglionic fibers from cells in these ganglia reach the smooth muscle or gland cells of the organ innervated. The action is usually antagonistic to that of the thoracolumbar innervation of the same organs.

The SACRAL VISCERAL EFFERENT OF AUTONOMIC system has the same general arrangement and functions as the cranial. The preganglionic fibers arise from cells in the 1st, 2nd, 3rd and 4th sacral segments of the cord and reach

terminal ganglia on or near the pelvic organs. Postganglionic fibers from cells in these ganglia terminate in the smooth muscle or glands of the organs, giving again an innervation antagonistic to the thoracolumbar autonomic. The chief pathways of the cranial and sacral autonomic systems are given in Table II.

THE RESPIRATORY MECHANISM

The visceral region of the medulla oblongata includes nerve connections which coordinate the various muscles concerned with respiration and regulate the rate of breathing. The term "respiratory center" has been applied to this mechanism, which was described by Legallois and Flourens (1847) as lying at the apex of the calamus scriptorius. It is no longer regarded as localized at this point,

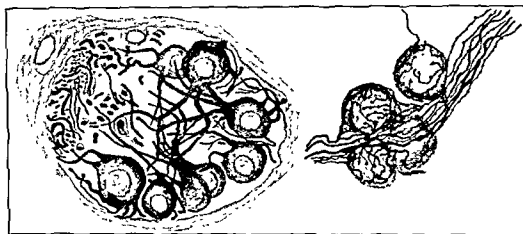


Fig. 108

Fig. 109.

FIG 108—SMALL GANGLION IN HUMAN LUNG. ROGERS METHOD.

FIG 109—GANGLION CELLS AND PERICELLULAR SYNAPTIC NETWORK.
METHYLENE BLUE STAIN.

but apparently includes several foci in the reticular formation of the medulla oblongata. Reticulospinal fibers carry impulses to the spinal cord. Fibers also have been described from the nucleus of the solitary tract which terminate in the cervical cord as a *solitariospinal tract*.

It has been demonstrated that the rate of respiration is affected by the amount of carbon dioxide in the blood reaching the medulla oblongata. The central mechanism is stimulated directly by excess of carbon dioxide, according to the results of Haldane, Gesell and others. It has been shown however that oxygen scarcity or excess of carbon dioxide in the blood produces, in addition, a peripheral effect by stimulating nerve endings in the lung and in the carotid sinus or carotid body. Such stimuli would reach the solitary tract through vagus fibers. They are then relayed to the coordinating mechanism where they are integrated with the various other stimuli received by it.

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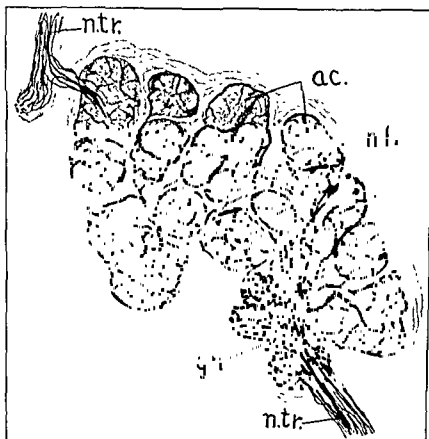


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THE VISCERAL SYSTEM

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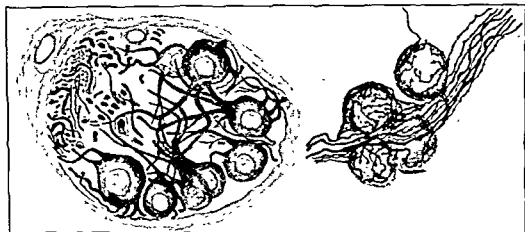


Fig 108

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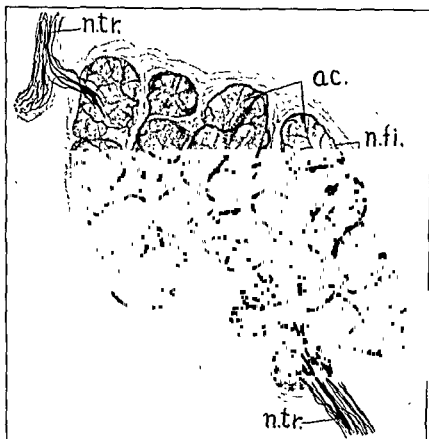


FIG. 107—NERVE ENDINGS IN HUMAN BRONCHIAL MUCOUS GLAND.

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VASOMOTOR PHENOMENA

Stimulation of the sympathetic trunk or section of the vagus nerve accelerates the heart rate. The effect of sympathetic stimulation is direct. Sectioning the vagus on the other hand removes the inhibitory action of the vagus centers. Conversely, section of the sympathetic branches to the heart or stimulation of the vagus retards the heart rate. Normally the cranial autonomic and the thoracic

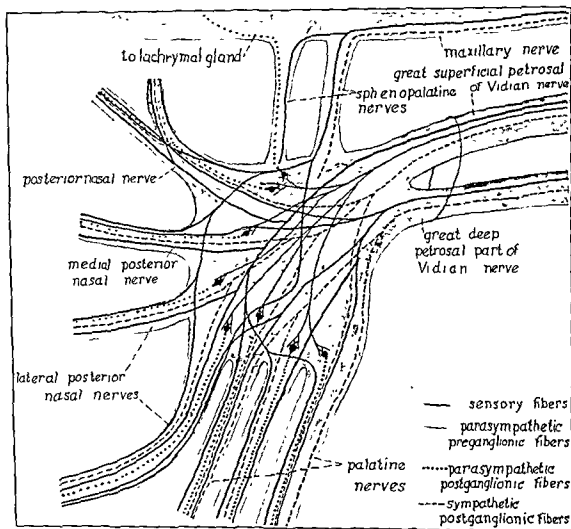


FIG 112—DIAGRAM OF THE SPHENOPALATINE GANGLION AND ITS CONNECTIONS.

columbar autonomic impulses to the heart are so integrated in the central nervous system as to produce the heart rate necessary to a given amount of body activity

Another effect of stimulating the sympathetic trunk is constriction of peripheral blood vessels and increased blood pressure. In the nasal region and in some of the pelvic organs vasodilator fibers also are present. These reach the organs concerned through the great superficial petrosal nerve and sphenopalatine

Section of both vagi results in permanent slow, deep breathing because of loss of impulses from the lungs which normally accelerate the respiratory rate. The respiratory mechanism of the medulla oblongata has usually been described as having an automatic activity but recent experimental studies indicate that peripheral stimuli from the lungs are necessary to respiratory rhythm as

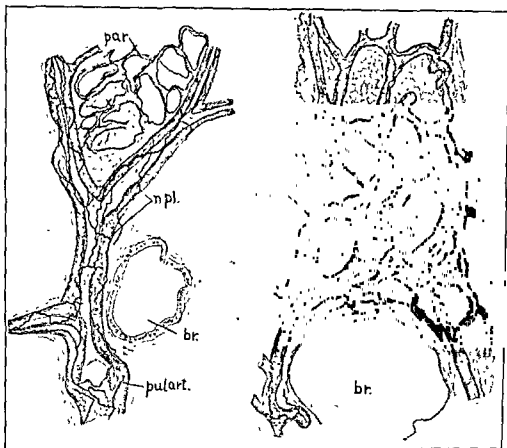


FIG 110

Fig. 111.

FIG. 110—VASOMOTOR NERVES ON PULMONARY ARTERIES

br., bronchus; *npl.*, nerve plexus, *par*, parenchyma of lung; *pulart.*, branch of pulmonary artery.

FIG 111—NERVE FIBERS ON PULMONARY CAPILLARIES.

br., bronchus, *cap.*, capillary plexus; *nfi.*, nerve fibers.

well as depth. There are two types of stimuli from the lung, one affecting the rate of breathing and the other affecting its depth. Several histological types of nerve endings in the lung have been demonstrated.

Strong stimulation of other sensory nerves, as the trigeminal endings of the nasal lining or free endings in the bronchial epithelium produce sneezing or coughing by violent coordinated action mediated by the respiratory center.

THE VISCERAL SYSTEM

THE ENTERIC PLEXUS

The digestive tube, like the heart, lungs and other visceral organs, has a double innervation, namely, craniosacral autonomic (parasympathetic) and thoracolumbar autonomic (sympathetic). In the wall of the tube there are two plexuses of nerve fibers with clusters of ganglion cells at their points of interlacement. One plexus lies between the longitudinal and circular layers of the muscular coat. It is known as the *myenteric plexus* or *plexus of Auerbach* (Fig. 114). The

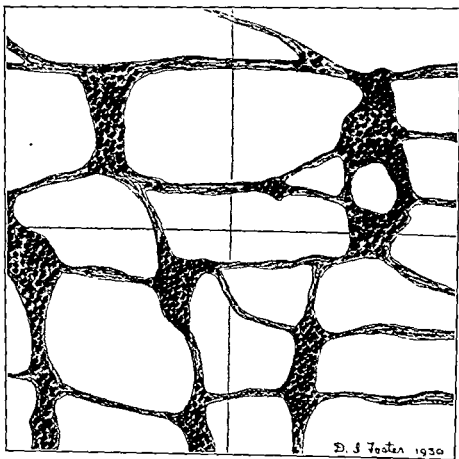


FIG. 114—AUERBACH'S PLEXUS AT MIDDLE THIRD OF DUODENUM.

Irwin, *Am J. Anat*, 1931, 49:152

second lies in the submucosa and is known as the *submucosal plexus* or *plexus of Meissner*. Both are made up of vagus fibers and fibers from the sympathetic ganglia, and of intrinsic ganglion cells and fibers arising from the latter. They are connected by bundles of fibers from one to the other plexus.

The myenteric plexus begins in the esophagus 30 to 40 mm. below the level of the larynx and continues to the internal sphincter in the lower part of the rectum. The submucosal plexus in the esophagus consists only of small bundles of nerve fibers of afferent type, without ganglion cell clusters. The fibers terminate in receptor endings in the epithelium or below it. In the stomach wall the

tine ganglion, in the case of the nasal membrane (Figs. 112 and 113) and through the pelvic nerve, in the case of the pelvic organs. Both of these nerves include parts of the craniosacral autonomic system.

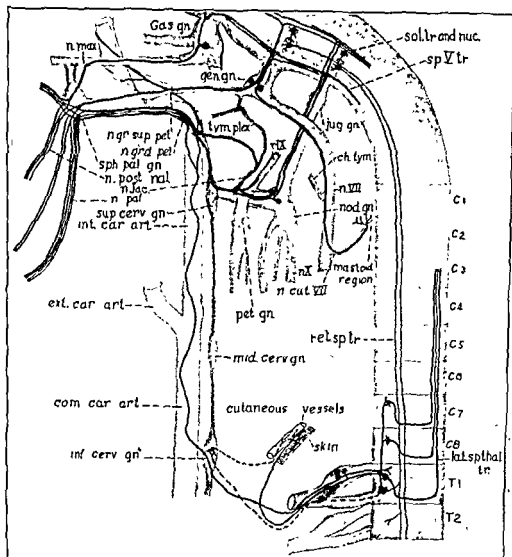


FIG 113—DIAGRAM OF SOME CONNECTIONS BETWEEN AFFERENT FIBERS OF CRANIAL NERVES AND VASOMOTOR FIBERS.

The question of vasodilators in the segmental nerves of the body is still unsettled. A considerable amount of evidence has accumulated pointing to the conclusion that such fibers, having their cells in the spinal cord, emerge through the dorsal nerve roots, and are distributed to the blood vessels.

THE VISCERAL SYSTEM

lation of the vagus excites secretion and stimulation of the sympathetic fibers inhibits secretion. The enteric plexuses must perform their normal functions reflexly, however, subject only to regulation by the nerves of external origin.

After bilateral section of vagus and splanchnic nerves to the intestine, local reactions to chemical or mechanical stimulation of the intestinal mucosa continue. These reactions are of the nature of coordinated reflexes. Rhythmic contractions also take place. The physiological data indicate a local coordinating nervous mechanism which can act independently of the central nervous system, to which the enteric plexuses are connected by the extrinsic fibers.

CLINICAL INTERPRETATION

HORNER'S SYNDROME

Lesions of the cervical sympathetic trunk may result in paralysis of the dilator fibers of the iris, with extreme contraction of the pupil (myosis); drooping of the eyelid (ptosis) from paralysis of the superior tarsal muscle; marked sinking of the eyeball (enophthalmus) from paralysis of the orbital muscle of Muller, a non-striated somewhat rudimentary muscle in the orbit across the infra-orbital groove and sphenomaxillary fissure. These ocular aspects of Horner's syndrome are accompanied by increased blood supply to the face, with redness and increased temperature, but with absence of sweating. The vasomotor effects are due to interference with the vasoconstrictor fibers of thoracolumbar autonomic origin. The absence of sweating is due to injury to the preganglionic fibers to the sweat glands of the face.

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submucosal plexus becomes prominent and continues as a marked plexus of fibers and ganglia into the intestine.

Various portions of the plexuses receive their extrinsic nerves from different parts of the sympathetic trunk and the parasympathetic outflow. The esophagus receives its sympathetic fibers chiefly from the inferior cervical ganglion. The stomach and small intestine receive sympathetic fibers from the coeliac ganglion. The appendix, ascending and transverse colon are supplied from the ganglia of the superior mesenteric plexus, and the descending colon from the inferior mesenteric plexus. The vagus supplies the parasympathetic element to the entire length of the digestive tube as far as the descending colon. The latter is supplied from the sacral autonomic through the pelvic nerve.

The vagus and pelvic nerve fibers form synapses with the ganglion cells, some ending in the first ganglion entered, while others pass to other ganglia of the myenteric plexus or to submucosal ganglia. The typical preganglionic and postganglionic fiber relationship appears to hold true in the digestive tube, as elsewhere, in the case of the vagus supply to the tube. The sympathetic fibers reaching the digestive tube are all postganglionic fibers from the various ganglia named. They are unmyelinated, while the preganglionic vagus fibers are myelinated.

The nerve cells of the myenteric plexus are chiefly multipolar and fall into two types, namely, *type I of Dogiel*, characterized by short dendrites, and *type II of Dogiel*, with long dendrites. The axons of type I extend for long distances within the plexus to adjacent ganglia, but do not leave the plexus. Type II cells send their axons to the muscle fibers of the muscular layer.

The ganglia of the submucous plexus are smaller and less numerous than in the myenteric plexus. Axons from their cells reach the muscularis mucosae. Some end in relation to muscle fibers, while others continue into the mucosa to end in relation to glands, smooth muscle fibers in the villi of the intestines, or among the epithelial cells. The dendrites of the submucosal cells are elongated, frequently extending beyond the ganglion in which individual cells are located.

In addition to the cells with direct vagus connections in the enteric plexuses, there are other cells which are regarded by some authors as belonging to an intrinsic and primitive nerve net. Others consider them as neurons of local synaptic reflex arcs. The entire question is much confused, but physiological evidence indicates the presence of a mechanism for local reflexes without reference to the central nervous system.

Afferent fibers pass through both plexuses to reach the epithelium, where they end between the cells. The advocates of a local reflex mechanism hold that processes of intrinsic nerve cells of the plexuses also reach the epithelium to receive stimuli.

Both vagus and sympathetic fibers have a rôle in movements of the digestive tube. Stimulation of the former excites peristalsis, while stimulation of the latter inhibits peristalsis. The secretory glands also have a double innervation. Stimu-

CHAPTER 11

THE GUSTATORY APPARATUS

The sense of taste belongs to the special visceral afferent system. It plays an important part both in selection of food and in reflexes having to do with digestive processes. While there are but four primary taste sensations, namely sweet, sour, bitter and salty, various combinations of these with olfactory stimuli of various kinds from foods give rise to recognition of flavors which are usually ascribed to taste.

The special receptors for taste are the taste buds (Fig. 115). They are clusters of neuro-epithelial cells found on the tongue, the soft palate and epiglottis (in embryos and in infants) and to some extent on the posterior wall of the oropharynx. Those on the tongue are embedded in the stratified squamous epithelium of the foliate and circumvallate papillae, especially, and to some extent on fungiform papillae.

The taste buds are ovoid masses of elongated cells embedded in the stratified squamous epithelium of the mouth cavity. On the sides of the circumvallate and foliate papillae, especially, they occur in groups. Each bud opens by a pore to the surface. The cells are of two types, both elongated, namely, *neuro-epithelial* and *sustentacular*. The neuro-epithelial cells are slender curved elements, somewhat rounded at the basal end and tapering toward the pore. The free end terminates in short processes which project into the deeper part of the pore but do not reach the surface. They are stimulated by substances in solution. When the tongue is dry, as after atropin, undissolved salt or sugar placed on the tongue does not give rise to the usual sensations of salty, sweet, etc.

Nerve terminals from the VIIth, IXth and Xth nerves end about the bases of the hair cells especially. Terminals have also been described about the so-called supporting cells. The VIIth nerve, through the chorda tympani (Fig. 116) supplies the taste buds on the anterior two-thirds of the tongue, the IXth nerve supplies those on the posterior third of the tongue, and the Xth nerve those on the epiglottis and pharyngeal wall. The last group of taste buds degenerate in late fetal life and early infancy, so that the gustatory nerves of the adult are the VIIth and the IXth.

The taste fibers from the anterior two-thirds of the tongue are supplied by the chorda tympani. Their cells lie in the geniculate ganglion and are typical unipolar sensory cells. The central processes enter the medulla oblongata through the intermediate nerve of Wrisberg and pass into the solitary tract, dividing

A TEXTBOOK OF NEURO-ANATOMY AND THE SENSE ORGANS

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THE GUSTATORY APPARATUS

are the same as for the IXth nerve. Secondary fibers from all these nerves arise from cells of the solitary nucleus, cross to the medial lemniscus of the opposite side and ascend to the higher centers of the brain, carrying stimuli which reach consciousness. These end in the hippocampal gyrus, but the specific region for gustatory sense is not known.

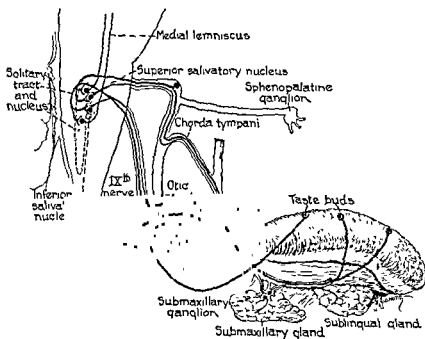


FIG. 116.—DIAGRAM OF GUSTATORY PATHS AND REFLEX CONNECTIONS.

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there into ascending and descending rami, which send collaterals and terminals into the nucleus solitarius.

Reflex connections are made from the solitary nucleus to the superior salivatory nucleus. Preganglionic fibers from the latter pass to the submaxillary ganglion, where they synapse with postganglionic fibers to the submaxillary and sublingual glands. Reflex connections to other motor and secretory centers are

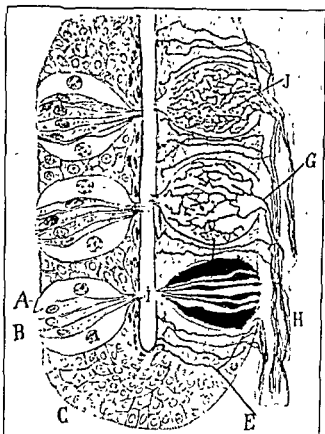


FIG. 115.—TASTE BUDS FROM FOLIATE PAPILLA OF TONGUE.

A, supporting cell; *B*, neuro-epithelial cells; *C*, stratified squamous epithelium; *E*, nerve fibers between the taste buds; *G*, nerve fiber endings within the taste buds; *H*, nerve bundles; *I*, pore; *J*, complete nerve fiber ending. After Retzius and Lenhossék. From Cajal, *Histology*, Wm Wood & Co, Baltimore, 1933

also made from the solitary nucleus, especially to the motor nuclei of the vagus for stimulation of gastric secretion.

The taste buds of the posterior third of the tongue and neighboring regions of the palatine arch are supplied by the IXth nerve. The fibers arise from cells in the petrous ganglion. The central processes enter the solitary tract and terminate in the solitary nucleus, with reflex connections similar to the VIIth nerve. Fibers from the Xth nerve supply the taste buds on the palate and epiglottis. These cells lie in the nodose ganglion, and their central reflex connections

THE VESTIBULAR APPARATUS

and the cochlea has begun to coil. By the 30 mm. stage the adult conditions (Fig. 120) have been reached, save that the utricle and saccule are not fully separated and growth is not completed.

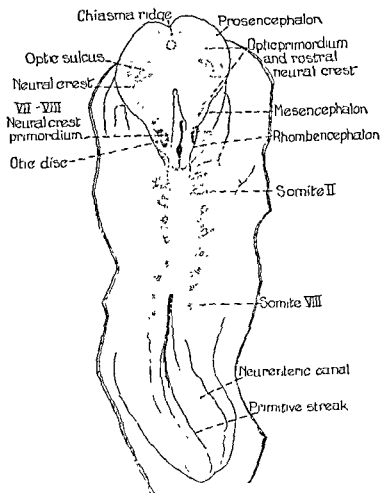


FIG. 117—DORSAL VIEW OF HUMAN EMBRYO OF 8 SOMITES, SHOWING OTIC DISC.

Redrawn from Bartelmez and Evans. Contributions to Embryology No. 85, Carnegie Institution of Washington, 1926.

ACOUSTIC NERVE

The nerves of the ear are derived from the VIIIth ganglion, which is formed from the neural crest. Nerve fibers from the ganglion cells, which retain the primitive bipolar condition, grow peripherally toward the labyrinth. Central processes in the meantime enter the medulla oblongata. The peripheral processes become arranged into two main bundles, a posterior cochlear division and an anterior vestibular division (Fig. 121).

The ganglion cells likewise eventually become segregated into two groups. One group becomes located around the central axis of the coils of the cochlea and is known as the *spiral ganglion* of Corti. The other becomes the *vestibular ganglion* of Scarpa. From the spiral ganglion peripheral fibers pass as a con-

CHAPTER 12

THE VESTIBULAR APPARATUS

The end organs of the vestibular apparatus consist of the *utricle*, the *saccul*e and the *semicircular canals*. The vestibular division of the VIIIth nerve, with its *vestibular ganglion* or *ganglion of Scarpa*, connects the end organs with the *vestibular nuclei* of the medulla oblongata. From these nuclei various central connections are made which enable the apparatus to perform its function. It is the apparatus primarily concerned with equilibrium and with muscle tone. Many of its activities are pure vestibular reflexes but others are performed in conjunction with reflexes originating in other sense organs, especially the eye. The vestibular system is a highly specialized part of the proprioceptive apparatus of the body.

DEVELOPMENT OF THE MEMBRANOUS LABYRINTH

The anlage of the membranous labyrinth appears in the human embryo of about eight pairs of mesodermic somites as a thickening of a portion of the ectoderm of the head (Fig. 117). A patch on each side at the level of the anterior part of the medulla oblongata becomes the *otic disc* (Fig. 118). In embryos of thirteen to fourteen pairs of somites the placodes become depressed into shallow pits. Subsequently the pits deepen and by the stage of twenty-three pairs of somites they have become transformed into otic vesicles which are nearly pinched off from the outside ectoderm.

The otic vesicle at first is nearly spherical. Very early a narrow prolongation from the upper part of the vesicle is recognizable (Fig. 119). This is the *labyrinthine recess*, which becomes the *endolymphatic duct* and *sac*. The dorsal part of the vesicle broadens while the ventral part narrows to a tapering structure. This becomes the *cochlea*, while the broad dorsal portion begins to show pouches which differentiate into the *semicircular canals*. These processes begin in an embryo of about four weeks (69 mm.). The anterior and posterior canals first appear from a pouch in the dorsal part of the vesicle. Somewhat later a laterally directed pouch appears from which the lateral canal is differentiated. As the pouches expand the thin plate of ectoderm, which results in the central region of each, presently degenerates and is replaced by mesoderm. The result is a semicircular ectodermal tube connected at each end with the main part of the vesicle (Fig. 119). This is well shown in an embryo of 20 mm. In the meantime the saccul and utricle have begun to differentiate from the common vesicle

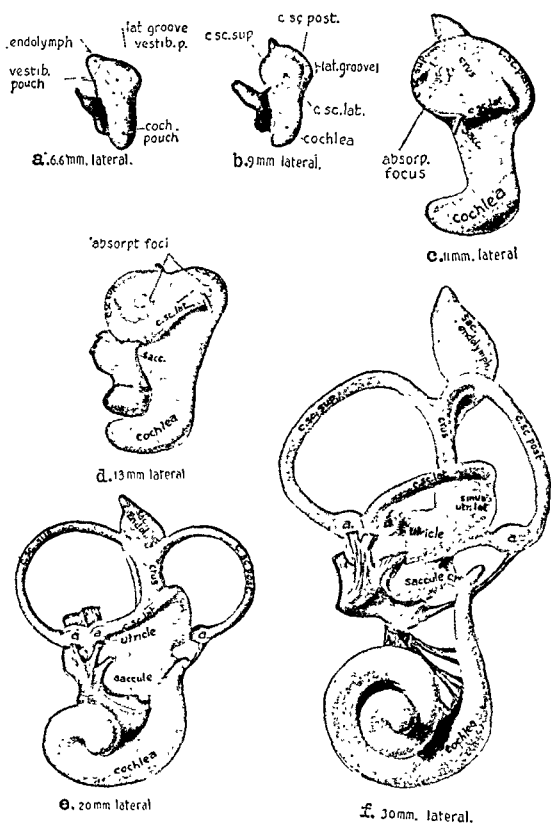


FIG 119.—LATERAL VIEWS OF A SERIES OF MODELS SHOWING DEVELOPMENTAL STAGES OF THE INNER EAR.

The age of the embryo is indicated below each figure. The colors blue and red are used to indicate respectively the cochlear and vestibular divisions of the acoustic ganglion. Nerve fibers can be distinguished from ganglionic masses by their lighter shade. $\times 25$. *absorpt. focus*, area of wall where absorption is complete; *a*, ampulla; *crus*, crus commune; *c.r.*, canalis reuniens; *c sc lat*, ductus semicircularis lateralis; *c sc post*, ductus semicircularis posterior; *c sc sup*, ductus semicircularis superior; *coch.*, or *cochlea*, ductus cochlearis; *sacc.*, saccule; *sac endol*, saccus endolymphaticus; *sinus utr lat.*, sinus utriculi lateralis; *vestib p*, vestibular pouch (From G L Streeter, *Am. J. Anatomy*, 1907, Vol 6)

tinuous spiral series into the organ of Corti of the cochlea. The vestibular ganglion gives off large bundles of fibers to the neuro-epithelial patches of the utricle and the saccule, and smaller branches to the cristae of the ampullae of each canal.

The VESTIBULAR NERVE consists of two parts, namely, the *ramus anterior* and the *ramus posterior*. The *ramus anterior* has its origin from the upper part of the vestibular ganglion. It is distributed peripherally to the macula of the utricle and the ampullae of the anterior and lateral semicircular canals, with a small twig to the macula of the saccule. The *ramus posterior* arises from the inferior part of Scarpa's ganglion. Its peripheral fibers pass to the macula of

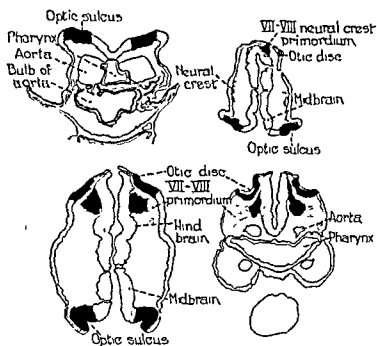


FIG 118—EARLY DEVELOPMENT OF OTIC VESICLE.

Redrawn from Bartelmez and Evans.

the saccule, to the ampulla of the posterior canal, and a small bundle of fibers joins the cochlear nerve. The connections of this bundle are obscure. The fibers to saccule, posterior ampulla and cochlea sometimes form a distinct division of the VIIIth nerve known as the *medial division*.

The COCHLEAR NERVE comprises the major portion of the posterior division of the VIIIth nerve. Its ganglion is located in the modiolus of the cochlea. Its peripheral fibers pass as a continuous spiral mass radiating from the ganglion into the organ of Corti. Here they end in relation to the sensory hair cells, forming calyx-like endings about the bases of these cells.

Experimental studies of pouch young of the opossum, in which the membranous labyrinth shows relatively early stages of differentiation at birth, have been of interest in interpreting the relation between development of the end

THE VESTIBULAR APPARATUS

bone, passing through a cartilage stage. This becomes the *bony labyrinth* within which the membranous labyrinth is protected. Within the cartilage-bony part there is formed three layers, a perichondrial, an intermediate and a membranous layer. The perichondrial layer becomes the internal periosteum, the intermediate layer is loose and disappears by transformation into perilymph, while the membranous layer forms the submucosa and supporting membrane of the epithelium.

The above is true of utricle, saccule and semicircular canals. In the cochlea there is the modification in that the central core or *modiolus*, and the bony shelf or *lamina* are formed directly as bone from fibrous connective tissue. The *basilar membrane*, extending from the spiral lamina to the opposite wall of the cochlea,

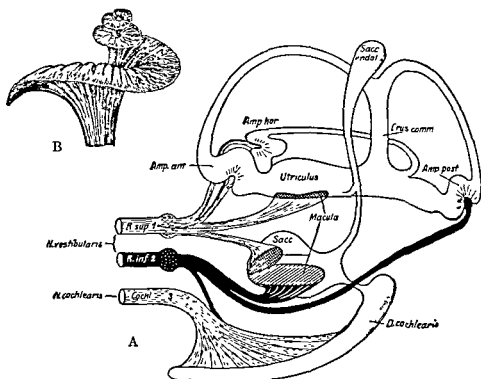


FIG 121 —NERVE SUPPLY OF THE INTERNAL EAR

A, diagram of distribution of nerves to the membranous labyrinth After de Burlet. B, the cochlear nerve After Arnold. Jackson-Morris, *Human Anatomy*, 9th ed, 1933

divides it into two spiral spaces. The upper one is further divided into a triangular *ductus cochlearis* and the *scala vestibuli* by the thin *Reissner's membrane*. The space below the *basilar membrane* is the *scala tympani*, which is continuous at the apex of the cochlea with the *scala vestibuli*.

BONY LABYRINTH

The end organs of the vestibular apparatus, together with the cochlea, are enclosed within the petrous bone. This bone is excavated into a series of cavities and canals known as the *bony labyrinth*. The largest and centrally placed cavity is the *vestibule*, the lateral wall of which is directed toward the tympanic cavity.

organs and the beginning of function. The opossum pouch young begins to show vestibular reflexes at about 43 days after birth. These reflexes are pronounced at 50 days. Histological study of the maculae and cristae indicate that beginning of functional activity in the vestibular apparatus is related to the proper stage of development of the hair cells and the otolithic membranes and cupulae. In stages which show hair cells surrounded by calyx-like nerve endings, but with short hairs and with little or no otolithic membrane, no functional response could be elicited. In later stages, beginning at 43 days, the degree of response appears in proportion to the development of the hairs and otolithic membrane, and to the number of hair cells apparently receiving stimuli.

Acoustic reflexes appeared at 50 days after birth, first in response to high,

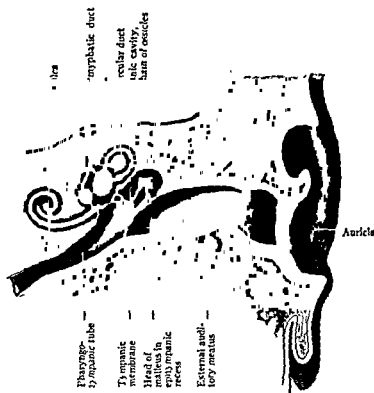


FIG 120—DIAGRAM OF PARTS OF THE HUMAN EAR.

From Cunningham, *Textbook of Anatomy*, Oxford University Press, London

shrill notes and on subsequent days, to lower notes. Correlated histological study of the developing cochlea indicates that as the different levels of the organ of Corti reach approximately the adult degree of differentiation, function begins. Differentiation of the organ of Corti is from the basal coil toward the apex. The sequence of response to notes of various pitch is in general agreement with other evidence on localization of tone reception in the organ of Corti. The central pathways of both vestibular and cochlear apparatus are well established before functional response can be elicited.

Soon after the otic vesicle is formed it is surrounded by mesoderm. The mesenchyme in proximity to the membranous labyrinth eventually develops into

THE VESTIBULAR APPARATUS

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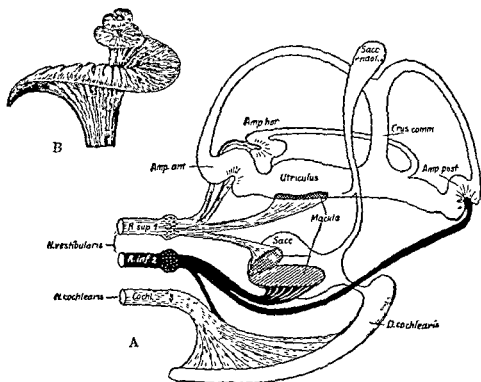


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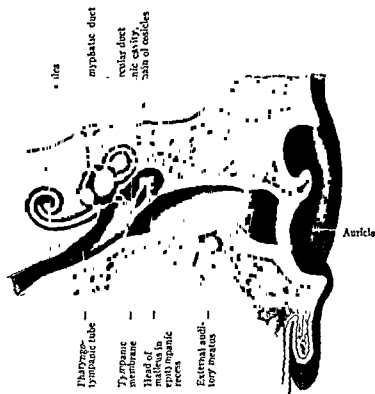


FIG. 120—DIAGRAM OF PARTS OF THE HUMAN EAR.

From Cunningham, *Textbook of Anatomy*, Oxford University Press, London

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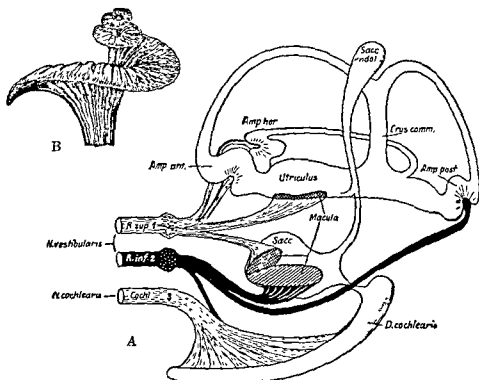


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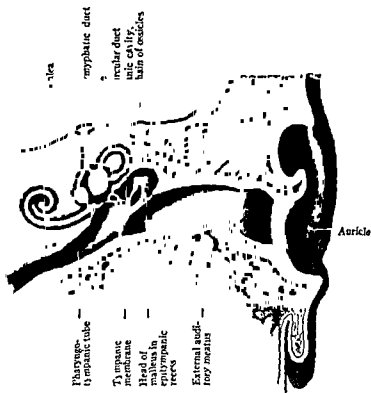


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THE VESTIBULAR APPARATUS

through the connections of these parts with the vestibule. The cavities and ducts of the membranous labyrinth contain *endolymph*.

The **UTRICLE** occupies the upper and posterior portion of the vestibule. The ampullae of the superior and lateral semicircular canals open into its upper portion, known as the *recess of the utricle*. The ampulla of the posterior canal opens into the *inferior sinus*, which is the lower and medial part of the utricle. The nonampullated end of the lateral canal opens into the central part of the utricle. The crus commune of the superior and posterior canals opens into the *superior sinus* which is an upward and posterior continuation of the utricle. In the floor and anterior wall of the utricular recess is found a patch of thickened epithelium and sensory cells, the *macula* of the utricle.



FIG 122—TRANSECTION OF THE MARGIN OF THE MACULA ACUSTICA SACCULI OF A GUINEA-PIG.

a, otolithic membrane; *b*, hairs; *c*, cuticular membrane; *d*, hair cells; *e*, sustentacular cells; *f*, epithelium of the saccule; *g*, tunica propria; *h*, nerve fibers; *i*, bone $\times 325$. (After Koelliker)

The **SACCULE** occupies the lower and anterior part of the vestibule. It is connected with the utricle by a small *utriculosaccular duct*, which arises from the medial side of the utricle. The utriculosaccular duct is joined by the *endolymphatic duct*, the two together joining the saccule. A short canal, the *ductus reuniens*, connects the anterior and lower part of the saccule with the *cochlear duct*. The endolymphatic duct enters the cranial cavity and expands into the *endolymphatic sac* which lies between the two layers of the dura. Endolymph is drained from the membranous labyrinth through the endolymphatic duct and sac, escaping into the subdural space. In the anterior part of the saccule lies the *macula acustica* of the saccule (Fig. 122), consisting of a thickened patch of epithelium and hair cells (Fig. 123).

It is ovoid in shape, measuring 6 mm. anteroposteriorly, 4 to 5 mm. vertically and 3 mm. transversely. Its long axis is directed forwards and laterally. The lateral wall of the vestibule is perforated by the *oval window* (*fenestra vestibuli*), which is covered by a membrane to which is attached the base of the *stapes*.

SEMICIRCULAR CANALS.—In front of the vestibule lies the *cochlea*, the base of which opens into the vestibule. The semicircular canals lie behind and above the vestibule. These are three in number, including a *superior*, a *lateral* and a *posterior* canal. Each canal forms two-thirds of a circle. They are somewhat compressed from side to side, and at one end of each canal there is a dilated portion known as the *ampulla*. The diameter of the bony canal is from 1 to 1.5 mm., and that of the ampullae is about 2 mm. The ampulla of each canal opens separately into the vestibule, that of the superior canal being the most anterior and lateral in position. The ampulla of the lateral canal lies just below that of the superior canal, while the ampulla of the posterior canal opens into the posterior and lower part of the vestibule. The nonampullated ends of the superior and posterior canals join to form a common canal (*crus commune*), which opens into the upper medial part of the vestibule. The nonampullated or medial end of the lateral canal opens into the vestibule between the *crus commune* and the ampulla of the posterior canal. The superior canal is placed in the vertical plane, transversely to the long axis of the petrous bone, with its convexity upward. It is 15 to 20 mm. long. The lateral canal is placed nearly in the horizontal plane, arching outward, and is 12 to 15 mm. long. The posterior canal, which is 18 to 22 mm. long, is vertical, arching laterally and posteriorly nearly at right angles with the superior canal. It makes an angle of nearly 45 degrees with the sagittal plane, as does the superior canal. The lateral canals of the two sides are found in nearly the same plane, and the superior canal of one side is nearly parallel to the posterior canal of the other side.

From the lower part of the vestibule, in front of the opening of the *crus commune*, there is the opening of the *vestibular aqueduct*. This is a small canal through the petrous bone, 8 to 10 mm. long, which is occupied by the *endolymphatic duct* and a small vein.

The bony labyrinth is lined with a thin membrane, the internal *periosteum*, which is also the immediate boundary of the cavities of the vestibule and the semicircular canals.

MEMBRANOUS LABYRINTH

The membranous labyrinth is enclosed by the bony labyrinth but does not fill the bony cavities. It is divided into *utricle*, *sacculle*, *semicircular canals*, with their *ampullae*, and the membranous portion of the cochlea. The latter will be further considered in connection with the organ of hearing. The space between the periosteum of the bone and the membranous labyrinth proper is filled with a fluid, the *perilymph*. This extends into the semicircular canals and cochlea.

THE VESTIBULAR APPARATUS

epithelium and hair cells. The latter have cilia 30 microns in length. Above the cluster of hair cells in each crista is found, in fixed material, a cone-like *cupula terminalis*, into which the cilia extend. Many histologists consider the cupulae to be fixation artefacts, since they are not apparent in fresh material. Nerve fibers from the vestibular nerve end as calyx-like terminations about the bases of the hair cells. Mechanical stimulation of the hairs of these cells, either directly by currents of endolymph or by the cupulae, after the latter have been set in motion by endolymph currents, give rise to nervous impulses in the hair cells. These are transmitted to the nerve fibers and through the vestibular nerve to the vestibular nuclei.

The MACULA ACUSTICA of the utricle and of the saccule are larger patches of sensory cells and epithelium. In both, as in the cristae of the ampullae, two kinds of cells are present, namely, *hair cells* and *supporting cells*. The latter branch at the deep ends and rest on the basement membrane. The hair cells are pear-shaped, the free end being truncated and ciliated, while the rounded basal ends lie between the supporting cells. Each is enclosed by a calyx of nerve fibers. The surface of the macula is covered by a plate of gelatinous substance in which are found small concretions of lime salts, known as *otoconia*, which, acted upon by vibrations and currents in the endolymph, stimulate the hair cells.

VESTIBULAR NUCLEI AND CONNECTIONS

The vestibular fibers divide into ascending and descending rami on entering the medulla oblongata. The ascending roots terminate in the *superior vestibular nucleus* (of Bechterew), in the homolateral *fastigial nucleus* of the cerebellum, in the cortex of the *flocculonodular lobe* of the cerebellum and in the *uvula*. These fibers constitute the *direct vestibular tract* to the cerebellum. Some of them take part in forming the *lateral commissure* of the cerebellum in lower vertebrates and mammals. This is probably true in higher mammals also.

The fastigial nucleus of the cerebellum is closely related to the vestibular nuclei both developmentally and functionally. It occupies a functional position intermediate between the vestibular nuclei and the other cerebellar nuclei.

The descending vestibular roots terminate in the *lateral vestibular nucleus* of Deiters, the *medial vestibular nucleus* of Schwalbe, and the *inferior or spinal vestibular nucleus*.

The four VESTIBULAR NUCLEI (Fig 84) lie in the somatic afferent column and extend from the level of the VIth nucleus to near the rostral end of the nucleus fasciculus gracilis. They are not sharply bounded from one another, but show differences in size and other characteristics of their respective neurons, and in their connections.

The SUPERIOR NUCLEUS of Bechterew is located in the floor and lateral wall of the rhomboid fossa and continues rostrally to the chief sensory Vth nucleus. It has multipolar neurons of medium size. The *lateral nucleus* of Deiters lies to

The MEMBRANOUS SEMICIRCULAR DUCTS (Fig. 124) are one-third to one-fifth the diameter of the bony canals. They are elliptical in cross section and are attached to the periosteum at one side of the bony canal. Their walls consist of a layer of connective tissue and a tunica propria lined within by a layer of flattened epithelium. The portion of the cavity of the bony canal not occupied by the membranous duct is filled with the perilymph. Frequently trabeculae of connective tissue from the wall of the membranous duct cross the perilymphatic space at various angles to unite with the periosteum of the opposite side. The bony canal is lined with mesothelium.

FIG. 123—NERVE ENDINGS IN THE MACULA ACUSTICA OF A GUINEA-PIG.

a, epithelium; b, tunica propria; c, three terminal nerve fibers Golgi stain. X about 200. (After Retzius.)

In the AMPULLAE of the bony canals are found the ampullae of the membranous ducts. In each ampulla there is a thickening of the tunica propria into a raised structure, the *transverse septum*. Upon this is found a *crista ampullaris* consisting of a patch of cubical and columnar

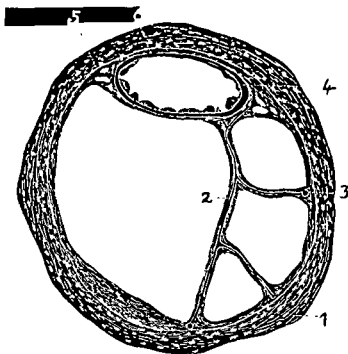


FIG. 124—TRANSECTION OF A HUMAN SEMICIRCULAR CANAL.

1, bone; 2, retiform connective tissue membranes; 3, at this point a band of connective tissue joins the periosteum; 4, membranous semicircular canal; 5, ligamentous attachment of the canal; 6, at this point the membranous and osseous canals are in contact. Moderately magnified. (After Rudinger.)

THE VESTIBULAR APPARATUS

impulses from higher centers. It has been shown that the vestibular nuclei must be intact for the rigidity to continue and Fulton suggests that these nuclei are released from control from higher cerebral centers by cutting of the extra pyramidal fibers in the operations which may cause it.

It has been shown that extensor tonus of muscles and positional reflexes are due to stimulation of the maculae acusticae of the membranous labyrinth by the otolithic membranes. The semicircular canals are not involved. Acceleratory reflexes, involving the eye (vestibular nystagmus) and skeletal muscles, arise in the semicircular canals. Righting reactions are complex phenomena involving labyrinthine reflexes in conjunction with proprioceptive impulses from neck and body muscles, the effects of body movements on the position of the head, and optical reflexes.

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the medial side of the restiform body at the level of entrance of the vestibular roots, and extends onto the lateral wall of the fossa. Its neurons are the largest found in the vestibular nuclei. The cell bodies are stellate in form and have long dendritic processes. The *medial nucleus* of Schwalbe, the principal vestibular nucleus, is larger than the others and lies below the principal part of the acoustic area, partly in the medulla oblongata and partly in the tegmental region of the pons. It consists of small stellate, triangular and spindle shaped cells scattered among the numerous vestibular fibers which enter the nucleus.

In addition to the direct vestibulocerebellar fibers already named, a *nucleocerebellar tract* passes to the fastigial nucleus, the cortex of flocculus, nodulus, uvula, and the anterior lobe, especially the lingula, of the cerebellum. These fibers arise principally in the superior vestibular nucleus. This nucleus also gives rise to fibers which enter the median longitudinal bundle of the same side to reach the eye muscle nuclei (Figs. 133 and 134).

The *median nucleus* gives rise to fibers which enter the opposite median longitudinal bundle to reach the eye muscle nuclei. It also gives origin to fibers which end in relation to cells of the *reticular formation* of the medulla oblongata. Impulses may be relayed hence to *reticulospinal* and other fibers. The *lateral nucleus* gives rise to the *lateral vestibulospinal tract* which descends into the same side of the cord. The *spinal vestibular nucleus* is described as giving rise to a crossed *ventral vestibulospinal tract*. Gray describes it as giving rise to fibers which descend into the cord in the median longitudinal bundle, some fibers extending the entire length of the cord. Fibers from the median nucleus appear to be included in the descending part of the median longitudinal bundles to the cord.

There is evidence of vestibular impulses to rostral parts of the brain stem, with relays to the cortex of the temporal lobe. Fibers to the thalamus and hypothalamus have been described, but there is little agreement as to their course. Experimental evidence indicates vestibular effects in the cortex of the temporal lobe. Stimulation of the vestibular labyrinth after increasing the responsiveness of the temporal gyri with strychnine produced convulsive movements. These no longer resulted when the vestibular nerve was cut.

The *median longitudinal bundle* is concerned with coördination of movements of the eyes and head in relation to maintenance of equilibrium. It contains, in addition to other fibers, descending vestibular fibers as follows: *homolateral vestibulomesencephalic fibers*, having their origin in the superior nucleus, *crossed vestibulomesencephalic fibers* from the lateral nucleus, and *lateral vestibulotegmental fibers* from the lateral nucleus to the reticular formation of the midbrain. Experimental studies have indicated that injury to the vestibulomesencephalic fibers results in circus movements of the animal. Injury to the lateral vestibulotegmental fibers produces rolling movements toward the injured side.

"Decerebrate rigidity" is a condition characterized by continuous spasm of the skeletal muscles, especially the extensors. It was interpreted by Sherrington who first described it in 1898, as a "release phenomenon" due to interruption of

AUDITORY APPARATUS

The ear bones are attached to each other by fine ligaments. The malleus, as already indicated, is attached by its manubrium to the inner surface of the tympanum. The base of the stapes is attached to the cartilaginous edges of an opening in the lateral wall of the bony labyrinth known as the *oval window*, or

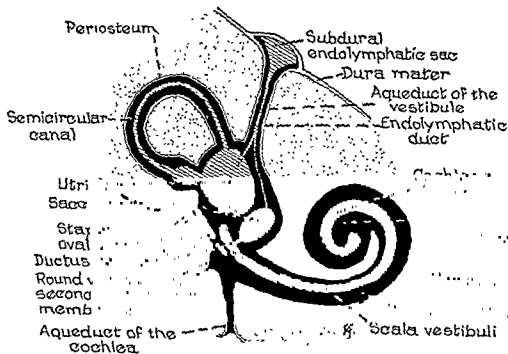


FIG. 125.—DIAGRAM OF PERILYMPHATIC AND ENDOLYMPHATIC SPACES OF INTERNAL EAR.

fenestra vestibularis, by a circular ligament. The vibrations of the tympanic membrane, amplified by the lever-like arrangement of the ear bones, impinge through the oval window on the perilymph in the scala vestibuli of the cochlea. Another opening in the bony labyrinth known as the *round window* or *fenestra tympanica* is located behind and below the oval window. A fibrous membrane across this window separates the tympanic cavity from the *scala tympani* of the cochlea.



FIG. 126.—AXIAL SECTION OF COCHLEA OF A FETAL CALF.

a, internal acoustic meatus, containing cut end of acoustic nerve as it enters modiolus. After Koelliker

The INNER EAR consists of the bony and the membranous labyrinth (Fig. 125), which terms also include the vestibular apparatus. Here, however, only the cochlea will be considered. This is a spiral tube of conical form (Fig. 126) with a basal diameter of 9 mm. and an axial length of about 5 mm. The bony canal is about 3 mm in diameter and about 35 mm. long. It makes two and one-half turns about its axis. It winds spirally about a cone-shaped bony core,

CHAPTER 13

AUDITORY APPARATUS

The auditory apparatus consists of external, middle and inner ear, the cochlear nerve, nuclei of the medulla oblongata in which this nerve ends, and the secondary tracts and nuclei for reflex connections and for transmission of auditory impulses to Heschl's gyrus of the temporal lobe of the cerebral cortex, the center of conscious hearing.

The EXTERNAL EAR (Fig. 120) or auricle is formed of a plate of elastic cartilage covered with skin and so shaped as to favor the direction of sound waves toward the external auditory meatus. The latter is protected by a waxy secretion, the cerumen, against invasion by insects, etc., into the canal. At the inner end of the auditory canal the *tympanum* is stretched across in such a manner as to receive those vibrations of the air which give rise to auditory stimuli. The *tympanum* is a thin, oval membrane with a thickened outer edge attached everywhere in a furrow in the bony wall of the meatus save at the anterior upper part. It is placed at an angle of 55 degrees with the floor of the canal. The outer surface of the tympanic membrane shows a marked concavity, the *umbo*, due to stretching by the *manubrium* of the *malleus*, which is attached to the inner surface of the membrane. The anterior, upper segment of the tympanum is thin and not stretched. This is called the *flaccid part*.

The outer surface of the tympanum is covered with thin, stratified, squamous epithelium. The inner surface is covered with flattened epithelium continuous with the mucosa of the tympanic cavity. Between these two epithelial layers the substantia propria of the tympanic membrane consists of two layers of collagenous fibers. The outer layer has a radial arrangement of its fibers. The inner layer has circularly arranged fibers. In the flaccid part there is only a very thin layer of loose connective tissue between skin and mucous membrane.

The MIDDLE EAR includes the tympanic cavity and Eustachian tube. The latter opens into the pharynx. The *tympanic cavity* is a space in the temporal bone whose lateral wall is formed by the tympanic membrane and the medial wall by the lateral surface to the bony labyrinth. It contains the three ear bones, namely malleus, incus and stapes, and two small muscles, the tensor tympani and stapedius, which are partly enclosed in bony tubes and attached to the ossicles. The chorda tympani, a division of the VIIth nerve, also passes through the cavity. The cavity is lined with squamous epithelium save at the opening of the Eustachian tube, where it is low columnar and ciliated, and at the border of the tympanic membrane, where the epithelium is cuboidal.

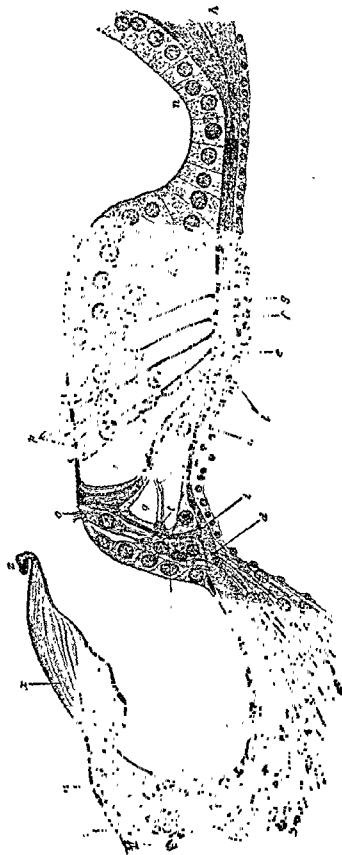


FIG. 128.—A RADIAL SECTION THROUGH CORTI'S ORGAN IN THE FIRST TURN OF THE HUMAN COCHLEA.

a, vestibular lip of the lamina spiralis, *b*, sulcus spiralis internus; *c*, epithelium of the sulcus, *d*, nerve fibers penetrating a foramen nervosum; *e*, mesenchymal epithelium of the scala tympani; *f*, fibrous layer of the basilar membrane; *g*, cuticular layer; *h*, spiral ligament; *i*, inner, and *h*, outer pillars; *l*, Deiters' cells; *m*, Hensen's cells, *n*, cells of Claudius, *o*, inner, and *p*, outer hair cells; *q*, Corti's tunnels; *r*, Nuel's space; *s*, nerve plexus among the inner hair cells; *t*, plexus within the tunnel; *u*, tunnel fibers; *v*, plexus about the outer hair cells, *w*, *x*, *y*, *z*, membrana tectoria $\times 465$. (After Koelliker.)

the modiolus, from which a bony shelf projects into the lumen. This is called the *bony spiral lamina*. At the apex of the cochlea, where the modiolus disappears, the bony lamina ends as a hook-like projection, the *hamulus*. The partition is extended from the margin of the bony spiral lamina to the opposite wall of the lumen by the *basilar membrane* (Figs. 127 and 128) which attaches to the periosteum of the outer wall of the cochlea along a thickened mass of connective

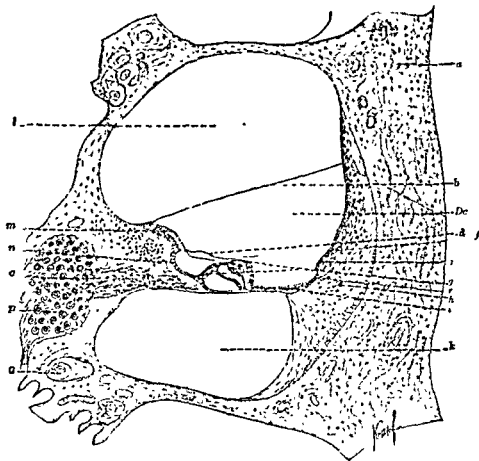


FIG 127—AXIAL SECTION THROUGH A TURN OF THE COCHLEA OF A GUINEA-PIG.

a, bone of the outer wall of the cochlea; *b*, membrane of Reissner; *d*, membrana tectoria; *De*, cochlear duct or scala media; *f*, stria vascularis; *g*, organ of Corti; *h*, spiral ligament; *i*, cells of Claudius; *k*, scala tympani; *l*, scala vestibuli; *m*, vestibular lip of the limbus spiralis; *n*, internal spiral sulcus; *o*, nerve fibers of the cochlear nerve, contained within one of the radiating canals within the osseous spiral lamina; *p*, nerve cells of the spiral ganglion; *q*, blood vessel; *r*, external spiral sulcus, upon which open Shambaugh's glands; *s*, prominentia spiralis, containing the vas promens (After Böhm and von Davidoff.)

tissue, known as the *spiral ligament*. The combined bony shelf and basilar membrane becomes gradually wider toward the apex of the cochlea.

The thin *membrane of Reissner* (Fig. 129) extends from the outer wall of the bony canal to pass obliquely downward medially and become attached to the spiral lamina. There are thus formed three spirally arranged cavities, best seen in cross

The ORGAN OF CORTI (Figs. 128, 129 and 130) consists of supporting cells and neuro-epithelial *hair cells*. Terminal fibers from the cochlear nerve, whose bipolar cells lie in cavities of the bony modiolus, radiate outward in a continuous sheet to terminate about the bases of the hair cells. The supporting cells are tall, slender elements which extend from their anchorage on the basilar membrane to the free surface of the organ of Corti, where they expand to form a cuticular plate, the *reticular membrane*, containing numerous openings in regular alternating rows. The hair cells rest in these openings. There are four types of supporting cells, namely, inner and outer phalangeal cells, which suspend the inner and outer

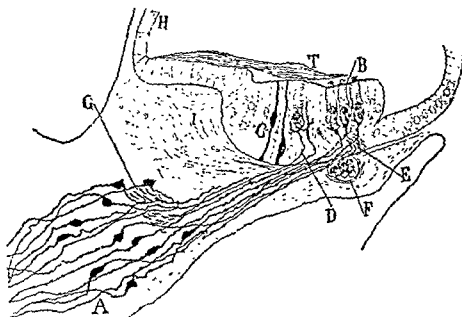


FIG. 130.—SECTION OF THE SPIRAL GANGLION AND OF THE ORGAN OF CORTI OF MOUSE. GOLGI METHOD (From Cajal)

A, bipolar cells of spiral ganglion, *B*, inner hair cells; *C*, supporting cells; *D*, terminal ending of an acoustic fiber, *E*, spiral nerve bundle, *F*, blood vessel; *G*, nerve fibers; *H*, Reissner's membrane, *I*, tectorial membrane.

hair cells respectively; the cells of Hensen, the cells of Claudius and the border cells

The *hair cells* are pear-shaped neuro-epithelial elements with cilia on their free ends. They occur as *inner hair cells*, on the axial side of the tunnel of Corti, in a single spiral row. The inner cells number about 3000. The *outer hair cells* occur in three rows in the basal coil, four in the middle and five in the apical coil, and number about 12,000. Attached to the vestibular lip of the spiral margin and extending over the hair cells of the organ of Corti is the *tectorial membrane*. It is made of delicate striated fibrils. Due to its susceptibility to distortion by fixing reagents the position of the tectorial membrane in the living cochlea is not clear. It is believed by many students of the ear that its lower surface is in contact with the hairs of the hair cells so that these are stimulated by movements of the membrane.

section of the bony canal. The upper cavity in such a section is the *scala vestibuli*, closed at its lower end by the base of the stapes. The lower space is the *scala tympani*, continuous with the *scala vestibuli* at the apex of the cochlea by an opening, the *helicotrema*, and closed at its base by the membrane of the round window. The third smallest canal is the *ductus cochlearis*, bounded above and medially by Reissner's membrane and resting on the basilar membrane and part of the bony spiral. The *scala vestibuli* and *scala tympani* contain perilymph, while

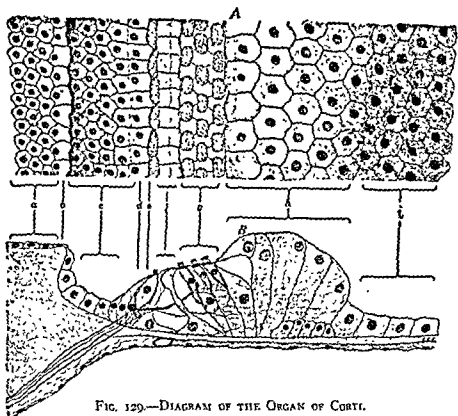


FIG. 129.—DIAGRAM OF THE ORGAN OF CORTI.

A, surface view, from the direction of the *scala media*; *B*, as seen in section, profile view, *a*, vestibular lip of the lamina spiralis; *b*, margin of same; *c*, sulcus spiralis internus; *d*, inner sustentacular cells, *e*, inner hair cells; *f*, pillar cells; *g*, outer hair cells and phalanges of Deiters' cells; *h*, cells of Hensen; *i*, cells of Claudius. Very highly magnified.

the cochlear duct, lined with ectodermal epithelium and containing the organ of Corti, contains endolymph.

The basilar membrane widens from base to apex of the cochlea. It is stretched between the tympanic lip of the periosteal border of the bony spiral lamina, internally, and the crest of the spiral ligament in the external wall of the bony canal. Upon it rests the organ of Corti. It is made up of three layers, the middle one constituting the *basilar fibers* or *auditory strings*. These are flexible when fresh and can be isolated. They increase in length with increased breadth of the basilar membrane from 64 to 128 microns in the first coil of the cochlea to 352 to 480 microns at the apex. They number about 24,000 in man.

CENTRAL CONNECTIONS

From the *dorsal cochlear nucleus* secondary fibers pass (1) to the *superior olive* (Fig. 132), (2) to the *accessory superior olive* and (3) to the *nucleus of the trapezoid body*. Other fibers pass with the *lateral lemniscus* both directly and crossed to the *nucleus of the inferior colliculus* in the midbrain. Many of the fibers from the *dorsal cochlear nucleus* cross just beneath the *inferior colliculus* and the *medial striae medullaris acusticae*, continuing into the *lateral lemniscus*, which is the secondary auditory tract, reaching the *inferior colliculus* and the *medial geniculate body*.

The *ventral cochlear nucleus* (Fig. 133) send fibers to the *olivary complex* of the same and the opposite side, also to the *nucleus of the lateral lemniscus* and to the *inferior colliculus* and *medial geniculate body* of the *thalamus*.

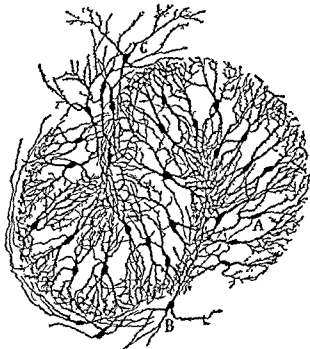


FIG 132—CELLS OF SUPERIOR OLIVARY NUCLEUS OF CAT GOLGI METHOD (From Cajal)

A, fusiform; B, marginal of anterior border; C, marginal of hilum.

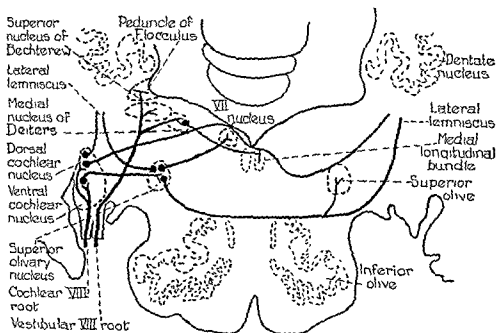


FIG 133—DIAGRAM OF AUDITORY AND VESTIBULAR CONNECTIONS IN MEDULLA OBLONGATA.

According to one theory of hearing, stimulation is by impact of the tectorial membrane on the hair cells, the membrane itself being set into vibration by waves in the endolymph of the cochlear duct. These in turn have been produced by vibration waves in the perilymph of the scala vestibuli through the action of the base of the stapes at the oval window. The waves of vibration are regarded as passing the length of the scala vestibuli, reaching the scala tympani through the helicotrema, and being finally dissipated in contact with the membrane over the round window.

Another view holds that the basilar membrane is made to vibrate by the waves in the perilymph. The rate of vibration, whether of tectorial or of basilar membrane, depends on the width of the membranes. Both become gradually wider from base to apex of the cochlea. The evidence indicates that notes of low pitch are received at the apex of the organ of Corti where these membranes are broadest, and that notes of increasingly higher pitch are received in successively lower sections of the cochlear coils. In the opossum pouch young the first note resulting in any reflex response was a high note (E'' , 1305 vibration cycles per second) at a developmental stage (50 days) where only the lower coil of the cochlea showed a histologically fully developed organ of Corti. During the succeeding seven days, concomitant with rapid differentiation of the remainder of the organ of Corti, the range of hearing, as determined by reflex responses, extended downward through three octaves to middle C (256 vibration cycles per second). Clinical observations on human patients indicate the same general arrangement.



FIG. 131—CHLs OF DORSAL AND VENTRAL COCHLEAR NUCLEI OF RABBIT GOLGI METHOD (Cajal.)

A, ventral cochlear nucleus; B, tail of nucleus; C, acoustic tubercle; E, restiform body; F, trigeminal nerve

The COCHLEAR NERVE fibers arise from cells in the spiral ganglion of Corti. This lies in the modiolus and winds about with the coils of the cochlea. The cells are bipolar and are about 30,000 in number in man. The peripheral processes, after losing their myelin sheaths, end about the bases of the hair cells as stated. The myelinated central processes enter the cochlear nuclei which lie lateral to the restiform body just as it turns upward toward the cerebellum. These nuclei (Fig. 131) are two in number, namely, a *dorsal cochlear nucleus* and a *ventral cochlear nucleus*. Some fibers appear to pass directly to the superior olivary nucleus.

CENTRAL CONNECTIONS

From the *dorsal cochlear nucleus* secondary fibers pass (1) to the *superior olive* (Fig. 132), (2) to the *accessory superior olive* and (3) to the *nucleus of the trapezoid body*. Other fibers pass with the *lateral lemniscus* both directly and crossed to the *nucleus of the inferior colliculus* in the midbrain. Many of the fibers from the *dorsal cochlear nucleus* cross just beneath the *inferior colliculus* and the *medial striae medullaris acusticae*, continuing into the *lateral lemniscus*, which is the secondary auditory tract, reaching the *inferior colliculus* and the *medial geniculate body*.

The *ventral cochlear nucleus* (Fig. 133) send fibers to the *olivary complex* of the same and the opposite side, also to the *nucleus of the lateral lemniscus* and to the *inferior colliculus* and *medial geniculate body* of the *thalamus*.

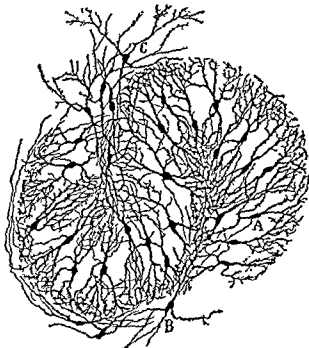


FIG. 132.—CELLS OF SUPERIOR OLIVARY NUCLEUS OF CAT GOLGI METHOD (From Cajal.)

A, fusiform; B, marginal of anterior border; C, marginal of hilum.

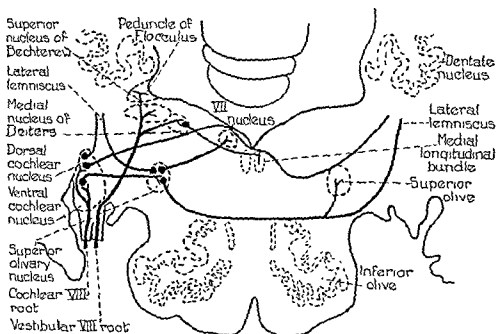


FIG. 133.—DIAGRAM OF AUDITORY AND VESTIBULAR CONNECTIONS IN MEDULLA OBLONGATA.

Fibers from the superior olive also pass to the nucleus of the VIth nerve and to the medial longitudinal bundles. In the latter they bifurcate, the ascending rami reaching the nuclei of the IIIrd and IVth nerves, and the descending rami reaching the cervical cord of the same side. These are reflex connections.

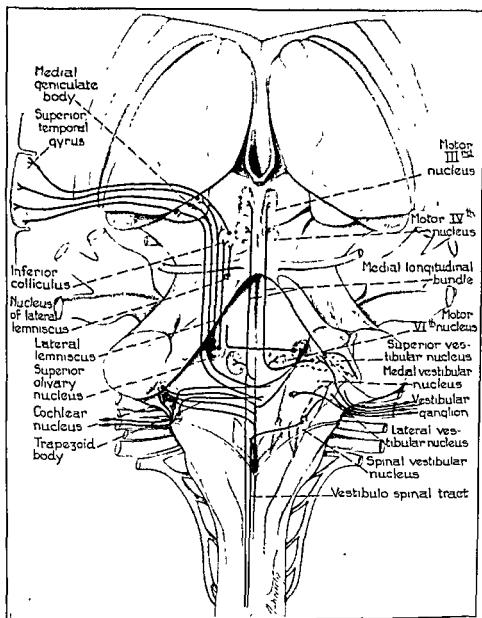


FIG. 134—DIAGRAM OF AUDITORY AND VESTIBULAR PATHWAYS

From the medial geniculate body impulses are relayed to the *superior* and *transverse temporal gyri* (Fig. 134) of the temporal lobe, where they end in the cortex. These gyri form the cortical projection area for conscious hearing. The medial geniculate bodies of the two sides are connected together by Gudden's

commissure, which accompanies the optic tracts, to cross just behind the optic chiasma.

The peripheral organ of the auditory system is differentiated from part of the older vestibular apparatus, hence the continuing anatomical relationship between them, although functionally the two have become entirely different. The central nuclei and pathways have also been differentiated from earlier existing lateral line and vestibular nuclei and generalized tracts, into the specific cochlear nuclei, superior olive, trapezoid body and lateral lemniscus, with their various connections.

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CHAPTER 14

PROPRIOCEPTIVE APPARATUS

Stimuli caused by muscular movement, tension on tendons and ligaments, motion and flexion of joints, position of members of the body, etc., are set up by special nerve terminations within the deep tissues of the body. The endings are of several histological types, but are grouped together as *proprioceptors*. The impulses initiated by them give rise largely to reflexes, but some reach consciousness. To what extent the latter should be differentiated from deep sensibility is not clear. Many of the myelinated nerve fibers entering striated muscle terminate as neuromuscular spindles or tendon spindles. Impulses from these and other proprioceptors, carried to the cord, brain stem and cerebellum, play an important part in coördination of muscular movement. For the sake of simplicity the apparatus primarily concerned with coördination of somatic reactions, as distinguished from deep sensory perception, will be described as a distinct system.

PROPRIOCEPTIVE TRACTS IN SPINAL CORD.—The nerve fibers to the proprioceptors are of the large, myelinated type, with large cells in the dorsal root ganglia in the case of those entering the spinal cord. The central fibers enter the dorsal funiculus through the dorsal roots (Fig. 66). They branch into ascending and descending rami. The latter pass down the cord one or two segments, and make reflex connections. The ascending fibers form an important part of the dorsal funiculus of the spinal cord. They terminate in the nucleus fasciculus gracilis and nucleus fasciculus cuneatus of the medulla oblongata (Fig. 135).

Some of the fibers, or collaterals from them, end in the intermediate region of the dorsal horn of gray substance. Here they make connections with cells whose axons form the ventral spinocerebellar tract. Others end in the nucleus dorsalis (Clarke's column), the cells of which give rise to the dorsal spinocerebellar tract. Still others make reflex connections between various levels of the spinal cord.

EXTERNAL ARCUATE FIBERS.—The proprioceptive impulses reaching the dorsal column nuclei of the medulla oblongata are relayed in part to the cerebellum and in part to other nuclei of the brain stem. Those to the cerebellum leave the nuclei as external and, possibly, internal arcuate fibers. *Dorsal external arcuate fibers* (Fig. 91) appear to have their origin largely from the *external nucleus of Monakow*, a somewhat isolated portion of the nucleus fasciculus cuneatus. It has larger cells than the main nucleus. It is regarded as corresponding to Clarke's column of the spinal cord, serving the muscles of the arm and

PROPRIOCEPTIVE APPARATUS

neck. Fibers from this nucleus reach the cerebellum of the same side through the restiform body. They appear to correspond to the dorsal spinocerebellar tract. *Ventral external arcuate fibers* are described by some authors as arising from

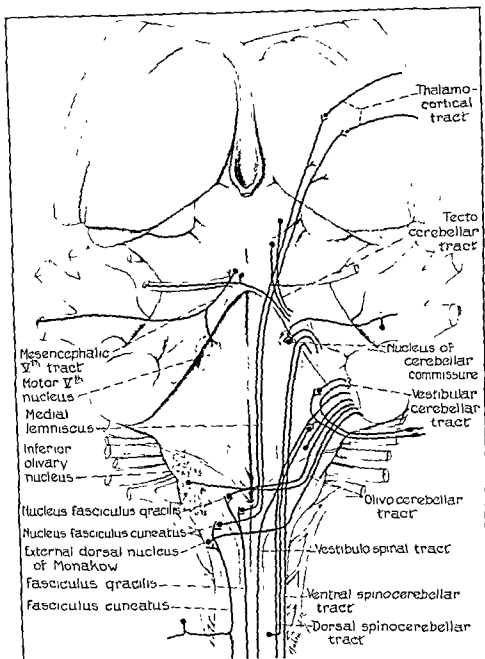


FIG. 135.—SOME PROPRIOCEPTIVE AND VESTIBULAR CONNECTIONS

the dorsal nuclei of the medulla oblongata and entering the medial lemniscus, after crossing the raphé. Others describe them as having their origin in the reticular formation of the medulla oblongata and reaching the cerebellum through the restiform body of the side opposite their origin.

CHAPTER 14

PROPRIOCEPTIVE APPARATUS

Stimuli caused by muscular movement, tension on tendons and ligaments, motion and flexion of joints, position of members of the body, etc., are set up by special nerve terminations within the deep tissues of the body. The endings are of several histological types, but are grouped together as *proprioceptors*. The impulses initiated by them give rise largely to reflexes, but some reach consciousness. To what extent the latter should be differentiated from deep sensibility is not clear. Many of the myelinated nerve fibers entering striated muscle terminate as neuromuscular spindles or tendon spindles. Impulses from these and other proprioceptors, carried to the cord, brain stem and cerebellum, play an important part in coördination of muscular movement. For the sake of simplicity the apparatus primarily concerned with coördination of somatic reactions, as distinguished from deep sensory perception, will be described as a distinct system.

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PROPRIOCEPTIVE APPARATUS

removing the restraint on the reflex which normally comes from the higher nervous centers.

In *tabes dorsalis*, characterized by degeneration of the nerve fibers of the dorsal funiculus, the proprioceptive impulses are unable to reach the higher coordinating centers in normal amount. The result is the failure of coördination of the muscles, as in walking, which is seen in locomotor ataxia.

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A TEXTBOOK OF NEURO-ANATOMY AND THE SENSE ORGANS

INTERNAL ARCUATE FIBERS (Fig. 91) relay proprioceptive impulses from the nuclei of the fasciculus gracilis and cuneatus through the medial lemniscus to the thalamus. From the latter the impulses may be relayed to conscious centers of the cerebral cortex. Internal arcuate fibers from the dorsal nuclei are also described as passing to the inferior olive. These connections, however, are not certain.

MESENCEPHALIC VTH TRACT AND NUCLEUS.—Large, unipolar cells are found scattered in the posterior part of the midbrain. They correspond structurally to dorsal root ganglion cells, and are regarded as sensory. They give rise to large myelinated fibers which emerge with the motor root of the Vth nerve. In their course through the tegmentum of the pons they give off collaterals to the motor Vth nucleus. Allen has shown that there are also cells of these fibers in the Gasserian ganglion and along the motor Vth root. The peripheral fibers pass chiefly, if not entirely, into the masseter muscle. They are regarded as proprioceptive for the muscles of mastication.

EYE MUSCLE AND TONGUE PROPRIOCEPTORS.—There is evidence, both histological and experimental, of proprioceptors in the external eye muscles. These play an important rôle in the maintenance of body position, etc. Muscle spindles have also been found in the tongue musculature, with fibers in the hypoglossal nerve (Langworthy, 1924). These undoubtedly have a part in the complex activities of the tongue, both in eating and in speaking.

MUSCLE TONUS.—In addition to proprioceptive impulses which reach consciousness and those which reach the cerebellum and other coördinating centers of the brain, the proprioceptive system has an important function in maintaining tonus of muscles. A muscle with normal connections with the spinal cord resists tension on its tendons due to movement of a joint or otherwise. This resistance is known as the stretch reflex. When a muscle is paralyzed by section of its dorsal or ventral roots it becomes flaccid. Impulses from proprioceptors within the muscle and tendon are set up by tension. These have been shown to be as frequent as 250 per second (Creed et al.). It is likely that a small amount of tension stimulates only a few receptors, while increase of tension brings more into action. Stimulation of a few receptors excites only a few motor neurons to reflex activity to counteract the tension. As more proprioceptors are stimulated more muscle fibers are reflexly affected, thus regulating the tension on the tendon.

KNEE-JERK.—A sudden and marked tension such as that produced by striking the patellar tendon, brings a large number of tension receptors into momentary activity. They send a simultaneous shower of impulses to the cord. By summation of central effect a large number of motor neurons are caused to discharge, producing the marked contraction of muscles resulting in knee-jerk. If the dorsal or ventral roots of the nerves supplying these muscles are injured the reflex does not take place. It is exaggerated if the upper motor neuron is injured, thus

Together they constitute the *cerebellar commissure*. In lower mammals and in submammals this arrangement is quite clear (Fig. 137). In higher mammals and in man it is obscured, save in certain stages of the embryo, by the wealth of cerebellar fibers of various origins.

Phylogenetically and in the mammalian embryo a layer of nerve cells and fibers forms along the course of the cerebellar commissure, giving rise to the second main division of the cerebellum, namely, the *corpus cerebelli* (Fig. 143). This receives the more general type of proprioceptive stimuli originating in muscles, tendons, etc., in contrast to the special vestibular stimuli which reach

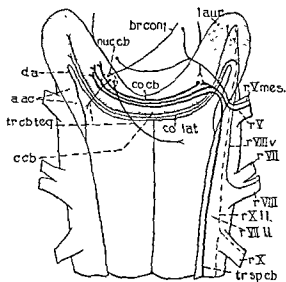


FIG. 136—DIAGRAM OF CEREBELLUM AND CEREBELLAR CONNECTIONS IN A NEWT (*Triturus*).

aac, acousticolateral area, *br conj*, brachium conjunctivum; *c.cb*, corpus cerebelli; *co cb*, cerebellar commissure, *co lat*, lateral commissure; *da*, anterior diverticulum of lateral recess of fourth ventricle, *laur*, auricular lobe, the forerunner of the mammalian flocculus, *nuc cb*, nucleus cerebelli, the forerunner of the deep cerebellar nuclei; *rV*, root of Vth nerve, *rVmes*, mesencephalic Vth root; *rVII*, root of VIIth nerve, *rVII l*, lateral line VIIth root; *rVIII v*, vestibular root of VIIIth nerve; *rX*, root of Xth nerve; *rX l*, lateral line Xth root, *tr cb teg*, cerebellotegmental tract; *tr. sp.cb*, spinocerebellar tract.

the flocculonodular lobe. The cerebellum thus consists of two fundamental structures, namely, the flocculonodular lobe and the corpus cerebelli, connected with the opposite sides of the rostral portion of the medulla oblongata by commissures.

In amphibians, with relatively sluggish movements, the corpus cerebelli is small in relation to the vestibular part of the cerebellum, i.e., the auricular lobe (flocculi of mammals). It increases in size in reptiles, birds, and mammals, becoming much folded in the latter two groups. Folding of the cortex begins in the larger reptiles, where a transverse fissure, the *fissura prima*, may be seen. This divides the corpus cerebelli into *anterior* and *posterior* lobes. In the alligator and small primitive mammals like the marsupial mole, the *fissura secunda*

CHAPTER 15

THE CEREBELLUM AND THE PONS

THE CEREBELLUM

The cerebellum is developed from the rostral region of the rhombencephalon as a suprasegmental organ. In its differentiation there have been two chief factors, namely, the vestibular and lateral-line systems on the one hand, and the trigeminal and spinal proprioceptor systems on the other hand (Fig. 136). The vestibular nerve roots, and in water forms the lateral-line root fibers also, send fibers of termination into the rostrolateral angle of the medulla oblongata. This region enlarges to form the auricular lobe of lower vertebrates, this becoming the flocculus of mammals. Between the two auricles there is found a commissural connection known as the *lateral commissure*. It contains direct and secondary vestibular fibers. In mammals this commissure lies in the zone of attachment of the nodulus to the base of the cerebellum and in the floccular peduncles. The nodulus is absent in submammalian forms, but in mammals the midcerebellar region, traversed by the lateral commissure, expands into the unpaired nodular formation. This is connected on each side by the lateral commissure with the paired flocculi, through the peduncles of the flocculi. In some mammals these peduncles consist merely of a bundle of nerve fibers, in others they are covered with a thin layer of cortex. In man patches of cerebellar cortex are occasionally found along the peduncles of the flocculi.

THE FLOCCULONODULAR LOBE

The vestibular part of the cerebellum, in mammals, includes the flocculi, their peduncles, and the nodulus. It constitutes the *flocculonodular lobe* which is bounded from the rest of the cerebellum by the *posterolateral fissure*. This is the first fissure to appear phylogenetically and also in the mammalian embryo.

THE CORPUS CEREBELLI

The deeper part of the rostral end of the rhombencephalon receives trigeminal fibers. Part of these end in a special part of the superior Vth nucleus, called the *nucleus of the cerebellar commissure*. Some of the trigeminal fibers, in amphibians, continue without interruption to the opposite side, forming a trigeminal commissure over the fourth ventricle. The direct fibers are augmented by secondary fibers from the nucleus of the cerebellar commissure and also by spinocerebellar fibers. These fibers are all members of the proprioceptive system.

THE CEREBELLUM AND THE PONS

given. The anterior lobe does not grow laterally to the same extent as does the posterior lobe. It is the most primitive part of the corpus cerebelli.

The **POSTERIOR LOBE** (Fig. 143) gives off lateral growths which result in the *paraflocculus* and in the *ansiform lobule* and its subdivisions. The *paraflocculus* is connected by a stalk with both uvula and pyramis. The *ansiform lobule* is a lateral expansion of the medial lobe of Ingvar, forming in man the greater part of the cerebellar hemisphere. The hemispheres in man are so expanded

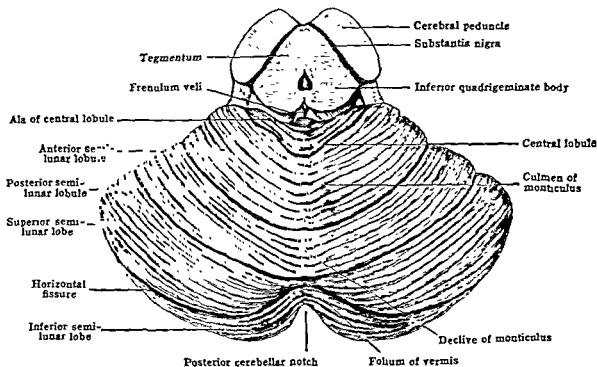


FIG 138—SUPERIOR SURFACE OF CEREBELLUM.

From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co., Philadelphia, 1933.

that there is formed a median zone between them, the *vermis*, which however consists in part of *flocculonodular lobe* and in part of distinct parts of the corpus cerebelli. It has no specific functional significance but the name is convenient as a descriptive term.

DEEP CEREBELLAR NUCLEI

The cerebellar nuclei consist in man of four paired gray masses buried in the mass of nerve fibers below the cerebellar cortex. The most medial is the *nucleus fastigii* or *roof nucleus*, which is also the oldest phylogenetically. Lateral to it lies the *nucleus globosus*, separated from the still more laterally placed *nucleus emboliformis* by a thin strand of white matter. In lower mammals these two nuclei are connected. Developmentally, and functionally they are one and should together be called the *nucleus interpositus*. Farther laterally lies the *nucleus dentatus* (Figs. 141 and 142), the largest of the group and much

divides the posterior lobe into two parts, the uvula and the *median lobe* of Elliot Smith. The posterior lobe is further subdivided in all other mammals by the *prepyramidal fissure* into *pyramis* and *median lobe of Ingevar*.

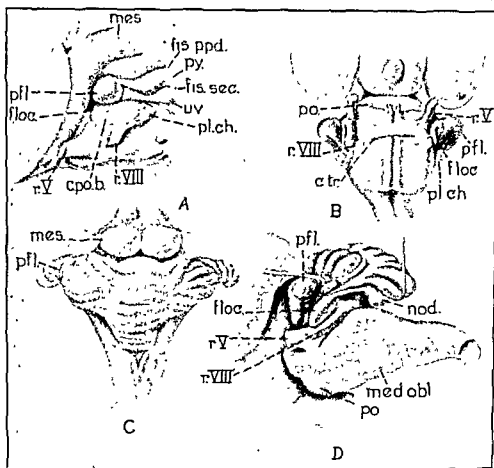


FIG. 137.—STAGES IN DEVELOPMENT OF THE CEREBELLUM OF THE OPOSSUM, TO SHOW RELATIONS OF FUNDAMENTAL PARTS IN A PRIMITIVE MAMMAL.

c.pob., pontobulbar body; *c.tr.*, trapezoid body; *fis ppd.*, prepyramidal fissure; *fis.sec.*, fissura secunda; *floc.*, flocculus; *med obl.*, medulla oblongata; *mes.*, midbrain; *nod.*, nodulus; *p fl.*, paraflocculus; *pl ch*, chorioid plexus; *po.*, pons; *py.*, pyramis; *r.V.*, root of Vth nerve; *r.VIII.*, root of VIIIth nerve; *uv.*, uvula.

A, lateral view of cerebellum and adjacent region of 30 day pouch young opossum. *B*, ventral view of medulla oblongata, pons, flocculus and paraflocculus of 30 day pouch young opossum. *C*, dorsal view of cerebellum and adjacent region of adult opossum. *D*, ventrolateral view of cerebellum and adjacent region of adult opossum.

The **ANTERIOR LOBE** (Fig. 143), is divided into *culmen*, *lobulus centralis* and *lingula*, each of which subdivides in larger mammals into smaller lobules and *folia*. The number of folds varies with the size and muscular development of the species. In man the folia are narrow and closely packed, resembling in sagittal section a sprig of cedar, from which fact the name *arbor vitae* was

THE CEREBELLUM AND THE PONS

fibers from the nucleus of the cerebellar commissure have already been described as part of this commissure.

The spinal connections (Fig. 146) are by means of *ventral* and *dorsal spinocerebellar tracts*. In the cat there has been described also an *intermediate spinocerebellar tract*, more closely related to the dorsal tract and entering the cerebellum through the restiform body.

The *ventral spinocerebellar tract* (Fig. 144) is the oldest phylogenetically. It appears to have its origin from cells in the dorsal horn and intermediate gray matter of both sides of the cord and ascends as a superficial bundle in the

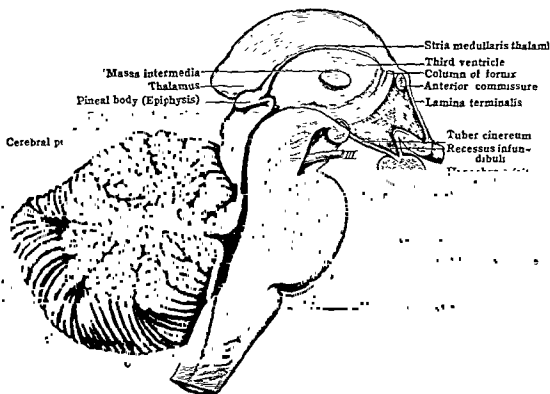


FIG 140—MEDIAN SECTION THROUGH CEREBELLUM AND BRAIN STEM.

From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co, Philadelphia, 1933.

lateral funiculus, reaching the cerebellum through the superior peduncle. It is distributed chiefly to the median (vermian) portion of the anterior lobe of the corpus cerebelli, carrying proprioceptive stimuli. While frequently called the tract of Gowers this usage is not strictly correct since Gower's tract includes also spinotectal and other fibers occupying the superficial lateral portion of the lateral funiculus.

The *dorsal spinocerebellar tract* (Flechsig's tract) (Fig. 144) arises from cells of Clarke's column (nucleus dorsalis) of both sides. The fibers enter the lateral funiculus in a zone just ventral to the tip of the dorsal horn. They turn upward and reach the cerebellum through the inferior peduncle. This tract is

folded in man and the apes. The dentate nucleus is not differentiated in sub-mammals. It is closely linked in its development with the appearance and growth of the neocerebellum and pons, with their connections from the cerebral cortex through the corticopontine and pontocerebellar tracts.

The cerebellar nuclei consist chiefly of large, multipolar cells (Fig. 142) whose axons pass to various parts of the brain stem. They receive fibers from various

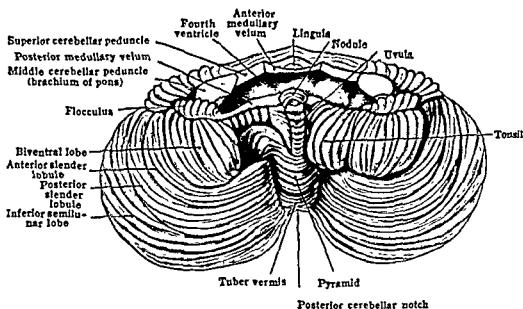


FIG. 139—INFERIOR SURFACE OF CEREBELLUM.

From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co., Philadelphia, 1933

parts of the cerebellar cortex, the individual paths of connection being described below

AFFERENT FIBERS OF THE CEREBELLUM

The incoming impulses to the cerebellum are derived from three main sources, namely, vestibular and trigeminal roots and nuclei, spinal cord, and cerebrum.

Vestibular root fibers (Fig. 145) enter the base of the cerebellum through the medial part of the restiform body and terminate in the cortex of the flocculonodular lobe and to some extent in the lingula and uvula.

Vestibulocerebellar fibers pass through the inferior cerebellar peduncle to be distributed to the entire basis cerebelli, to the greater part of the anterior lobe and to the uvula. These are secondary fibers from the vestibular nuclei, especially from the superior nucleus of Bechterew and also the lateral nucleus of Deiters.

Trigemino-cerebellar fibers have not been demonstrated in man or higher mammals but are clearly present in lower mammals (Fig. 144) and sub-mammals. *Direct trigeminal fibers* are few or lacking in mammals. Secondary

strated in higher mammals or man, probably because hidden by the wealth of other fibers. If, as has been suggested, it conveys impulses from the visual centers to the cerebellum, it should be present in higher mammals and man, in which the visual centers are very important.

Reticulocerebellar fibers from the reticular substance of the medulla oblongata have been described. They arise from cells of the lateral and inferior reticular nuclei.

EFFERENT FIBERS

The efferent cerebellar fibers have their origin chiefly in the deep nuclei. Some however arise from cells of the flocculus. There are three principal

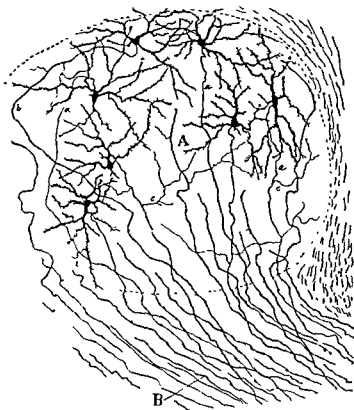


FIG 142—CELLS OF THE DENTATE NUCLEUS FROM CAT FOETUS. GOLGI METHOD

A and *B*, fibers of the superior cerebellar peduncle; *a*, *b*, axons of cells of dentate nucleus, *c*, collaterals. (From Cajal)

bundles, namely, the angular bundle of Lowy, the uncinate bundle of Russell and the brachium conjunctivum (Fig. 149).

The *angular bundle of Lowy* probably represents axons of Purkinje cells of the flocculus. It enters the medulla oblongata at the angle of the lateral recess and ends in the vestibular nuclei. It represents, apparently, the oldest efferent connection of the cerebellum.

The *uncinate bundle of Russell* (*cerebellovestibular and spinal tract*) has its origin in the fastigial nuclei of both sides. Fibers from the globose nucleus

distributed to the anterior lobe, the pyramis and the uvula, terminating somewhat more laterally than the ventral spinocerebellar tract.

Olivocerebellar fibers enter the cerebellum from the inferior and accessory olivary nuclei of the opposite side and to some extent from the same side. These may be regarded as *internal arcuate fibers*. They pass through the restiform body.

Dorsal and ventral external arcuate fibers also reach the cerebellum. The dorsal external arcuates arise largely from the nucleus cuneatus of the same side and pass directly through the restiform body to the cerebellum. The ventral external arcuates have their origin in the nucleus gracilis, the nucleus cuneatus,

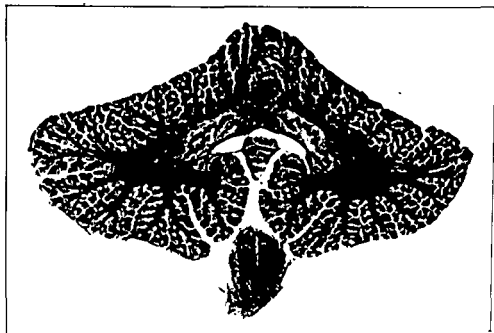


FIG 141—HORIZONTAL SECTION OF CEREBELLUM, SHOWING DENTATE NUCLEUS.

the arcuate nuclei and the lateral reticular nucleus. They cross the midplane and sweep around the olive, forming a thin layer external to it, to pass through the restiform body of the opposite side into the cerebellum.

Pontocerebellar fibers constitute the middle cerebellar peduncle or brachium pontis. They arise from the pontine nuclei, cross the midplane ventrally and ascend to terminate in the cerebellar hemispheres. Those arising from the rostral portion of the pons pass to the inferior part of the hemispheres. Those from the lower portion of the pons pass to the upper part of the hemisphere. The pons and its cerebellar connections are present only in mammals and man. They constitute the most recent connections of the cerebellum, phylogenetically.

Tectocerebellar fibers enter the cerebellum of submammals and lower mammals through the anterior medullary velum. This tract has not been demon-

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The surface of the cerebellum is folded into large numbers of narrow gyri or folia. Each folium consists of a core of medullary substance and a cortex composed of three layers, namely, a *granular layer*, adjacent to the medullary substance, a layer of *Purkinje cells*, and an outer *molecular layer* (Figs. 147 and 148). The structure of the folia is the same in all parts of the cerebellum

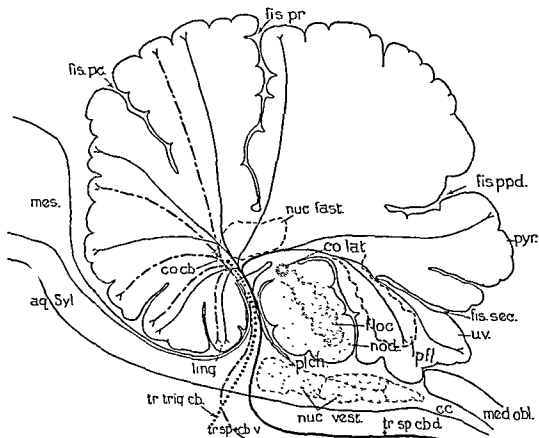


FIG. 144—DIAGRAM OF SPINOCEREBELLAR AND TRIGEMINAL CONNECTIONS OF CEREBELLUM

aq., aqueduct of Sylvius, *cc.*, central canal; *co. cb.*, cerebellar commissure; *co. lat.*, lateral commissure, *fis. pc.*, preculminate fissure, *fis. pld.*, prepyramidal fissure, *fis. pr.*, fissura prima; *fis. sec.*, fissura secunda, *fis. po. lat.*, posterolateral fissure, *floc.*, flocculus; *ling.*, lingula; *lob. sim.*, lobulus simplex, *lob. med. ling.*, medial lobe of Lingvar; *mes.*, midbrain, *nod.*, nodulus, *nuc. dent.*, dentate nucleus; *nuc. fast.*, fastigial nucleus; *nuc. int.*, interpositus nucleus; *nuc. vestib.*, vestibular nuclei, *pfl.*, paraflocculus, *pl. ch.*, chorioid plexus; *pyr.*, pyramis; *tr. d. vestib.*, direct vestibular tract to cerebellum; *tr. vestib. cb.*, vestibulocerebellar tract, *tr. sp. cb. d.*, dorsal spinocerebellar tract, *tr. sp. cb. v.*, ventral spinocerebellar tract; *tr. trig. cb.*, trigeminocerebellar tract; *uv.*, uvula, *v. 4*, fourth ventricle.

The *granular layer* consists of numerous small cells, the granules, which have three to six short dendrites, and a single axon. When stained by ordinary histological methods the cells appear rounded and the nuclei are seen to nearly fill the cell body. The dendrites terminate in peculiar, short, claw-like branches within the granular layer. The axons, which are unmyelinated, pass toward the surface to enter the *molecular layer*. Here they bifurcate, one branch run-

have also been described. The fibers hook over the brachium conjunctivum and descend in the inferior cerebellar peduncle to terminate, chiefly, in the vestibular nuclei. Some fibers end in the reticular formation. Others continue into the cervical region of the spinal cord.

The *fastigiobulbar tract*.—In addition to the hooked bundle of Russell there is a direct tract from the fastigial nuclei to the medulla oblongata. It also descends through the inferior cerebellar peduncle and terminates in the vestibular nuclei and the reticular formation.

The *brachium conjunctivum* takes origin from the dentate, emboliform and globose nuclei and passes rostrally and ventrally into the midbrain. After cross-

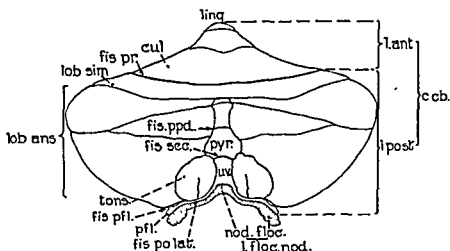


FIG. 143—DIAGRAM OF HUMAN CEREBELLUM.

c.c.b., corpus cerebelli; *cul.*, culmen; *fis pfl.*, parafloccular fissure; *fis polat.*, posterolateral fissure; *fis ppr*, prepyramidal fissure; *fis pr*, fissura prima; *fis sec.*, fissura secunda; *l. ans.*, ansiform lobule; *l. flocc. nod.*, lateral floccular nodule; *pfl.*, paraflocculus;

ing as the decussation of the brachium conjunctivum, part of its fibers end in the red nucleus. A large number, however, continue forward to terminate in the lateroventral nucleus of the thalamus, giving collaterals to the red nucleus. There is evidence that some brachium conjunctivum fibers end in the tegmentum of the midbrain and of the medulla oblongata as cerebellotegmental fibers.

HISTOLOGY OF THE CEREBELLUM

The cerebellum is made up of an outer gray layer, the *cortex*, and a deeper lying *medullary portion*. Embedded within the latter are found the gray masses of the cerebellar nuclei, made up of large multipolar neurons. The medullary portion proper consists chiefly of great numbers of myelinated nerve fibers which represent the afferent and efferent fibers of the cortex.

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rounded base, from which the axon is given off, and a tapering body which divides into one to three dendrites. The dendrites are large near the cell body, but branch into large numbers of smaller processes which extend toward the cerebellar surface in the *molecular layer*. Typically they spread out fan-like from the cell, the dendritic processes from each Purkinje cell occupying a broad but thin zone whose axis lies at right angles to the major axis of the

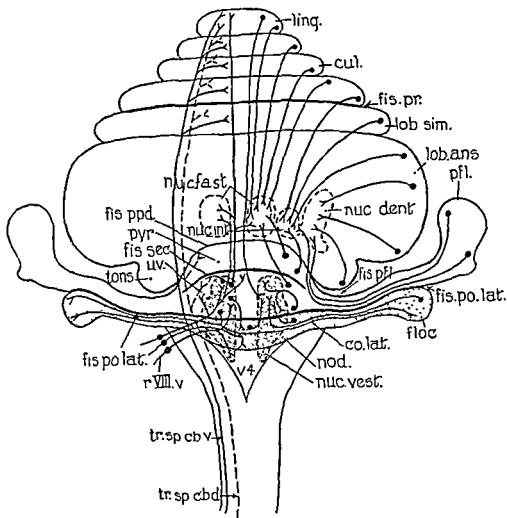


FIG. 146.—DIAGRAM OF CEREBELLAR CONNECTIONS.

See Figure 144 for abbreviations.

folium By this arrangement tremendous numbers of axonic processes from the granule cells, which, as above indicated, have a course parallel with the main axis of the folium, pass through the spread of Purkinje cell dendrites and come into synaptic relation with them. The axons of the Purkinje cells pass into the medullary substance and reach the deep cerebellar nuclei. Purkinje cells in the flocculus, however, give off axons which reach the vestibular

THE CEREBELLUM AND THE PONS

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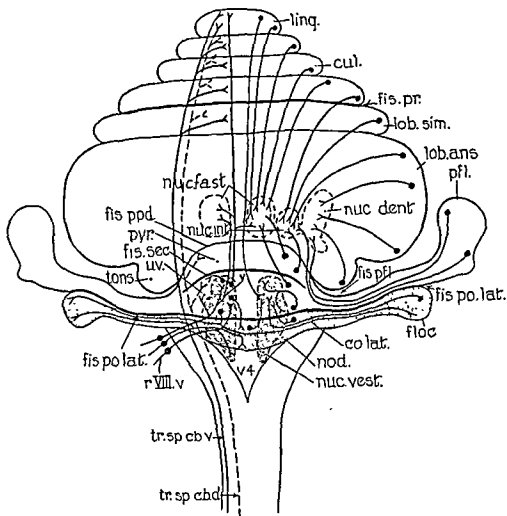


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nuclei. Near the cell body the axons have numerous collateral branches which effect connections with neighboring Purkinje cells.

The *molecular layer* consists chiefly of the granule cell axons and Purkinje cell dendrites already described, but also many climbing fibers enter it from the medullary substance. The climbing fibers twine about the Purkinje cell den-

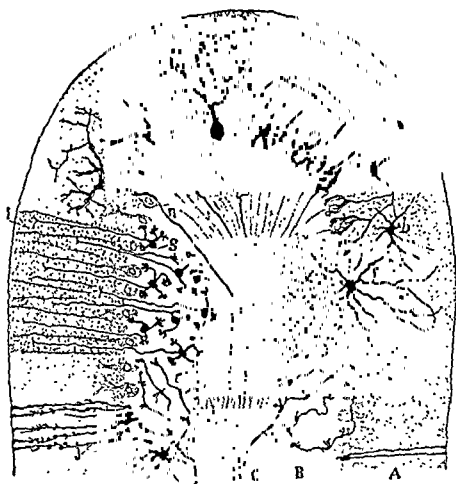


FIG. 147.—SEMIDIAGRAMMATIC TRANSVERSE SECTION OF A CEREBELLAR LAMELLA, GOLGI.

A, molecular layer, *B*, granular layer; *C*, medullary layer; *a*, Purkinje cell; *b*, basket cells with *d*, basket-like synapses on bodies of Purkinje cells; *c*, superficial stellate cells; *f*, Golgi type II cell; *g*, granule cells, with *i*, bifurcating axons; *h*, mossy fibers; *j*, and *m*, neuroglia; *n*, climbing fiber Golgi method From Cajal, *Histology*, Wm. Wood & Co, Baltimore, 1933.

drites, ramifying with the latter and forming synapses, apparently through the gemmules with which the dendrites of the Purkinje cells are studded.

Two types of nerve cells also are found in the molecular layer. The *basket cells* lie for the most part in the deeper portion of this layer. These are stellate in form, with four to six relatively short dendrites radiating from the cell body, and with a single axon which gives off a large number of collaterals, each forming a synaptic basket about the body of a Purkinje cell. In the outer zone

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of the molecular layer are found smaller stellate cells each having a few dendrites and an axon which runs parallel with the surface of the folium, but at right angles to its main axis.

Two principal types of fibers reach the cerebellar cortex, namely, the *climbing fibers* and the *mossy fibers*. The latter end in the granular layer, each fiber forming synapses with large numbers of granule cells. The impulses are relayed by the axons of these cells to the Purkinje cells, large numbers of these having synaptic relations with each parallel fiber formed by these axons. In this way

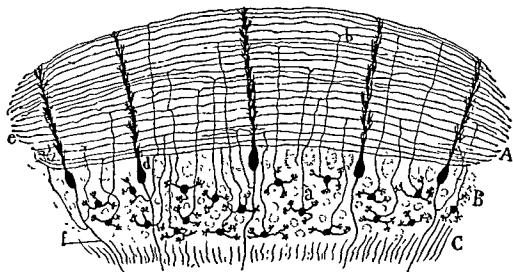


FIG. 148—LONGITUDINAL SECTION OF A LAMELLA OF CEREBELLUM.

A, molecular layer, *B*, granular layer; *C*, medullary layer; *a*, axon of granule cell; *b*, its bifurcation in the molecular layer, *c*, terminations of parallel fibers; *d*, Purkinje cell. Golgi method. From Cajal, *Histology*, Wm Wood & Co, Baltimore, 1933

the impulses entering through the mossy fibers are very widely diffused in the cerebellum. The climbing fibers end in relation to individual Purkinje cells. By means of the collaterals, above described, impulses from one Purkinje cell may affect many others in its neighborhood. Also the basket cells, through their connections with large numbers of Purkinje cells, may excite these to simultaneous action. The entire cerebellar mechanism is so arranged as to favor the diffusion of stimuli throughout the cortex, the summation and reinforcement of these stimuli, and prolongation of motor discharge. The "avalanche conduction" of Cajal is particularly favored by the arrangement of the cerebellar elements

Climbing fibers appear to enter the cerebellum most numerous through the brachium pontis, while the mossy fibers enter chiefly through the restiform body.

CONNECTIONS OF THE CORTEX

The connections of the cerebellar cortex are with the deep cerebellar nuclei, the vestibular nuclei and the reticular formation of the medulla oblongata. The

flocculonodular lobe sends efferent fibers to the vestibular nuclei. Dow (1936 and 1938) has shown that fibers from the flocculus end in the lateral nucleus of Deiters and the superior nucleus of Bechterew. The nodulus sends fibers to all the vestibular nuclei, to the reticular formation of the medulla oblongata and some to the fastigial nucleus. A few enter the medial longitudinal bundle.

The cortex of the corpus cerebelli (Fig. 146) gives efferent fibers to the nucleus interpositus and the nucleus dentatus. Experimentally it has been shown that efferent fibers from the anterior lobe and from the lobulus simplex, the

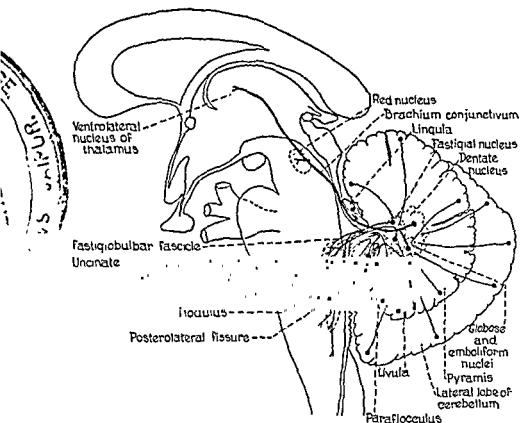


FIG. 149.—DIAGRAM OF EFFERENT CEREBELLAR CONNECTIONS.

pyramis and the uvula of the posterior lobe enter the fastigial nucleus. From the culmen, lobulus simplex, pyramis, paraflocculus and crus I of the ansiform lobule they enter the nucleus interpositus. From the median lobe of Ingvar, including the ansiform lobule, and in part from the paraflocculus, they enter the dentate nucleus.

The *fastigial nucleus* gives rise to the fasciculus uncinatus of Russell, which hooks over the brachium conjunctivum and passes into the medulla oblongata by way of the restiform body, to terminate in the vestibular nuclei and the reticular formation of the bulb and cord, as stated above.

The *nucleus interpositus* (*globose and emboliform nuclei*) and *nucleus den-*

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tatus together give rise to the *brachium conjunctivum*. This passes forward as the superior cerebellar peduncle and ends, in part, in the red nucleus of the midbrain, and in part, in the lateroventral nucleus of the thalamus.

THE PONS

The pons is the region of the brain which connects the medulla oblongata, the cerebrum and the cerebellum. Externally it appears as a broad, transverse

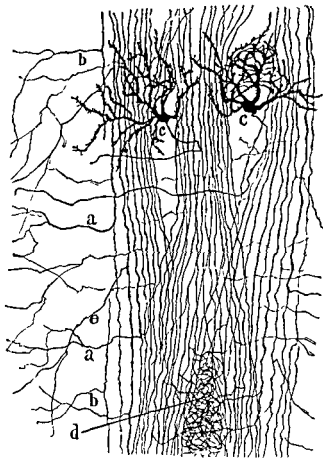


FIG 150—CELLS AND FIBERS OF PONS OF KITTEN GOLGI METHOD (From Cajal)

a, collaterals from fibers of pyramids; *b*, other collaterals; *c*, cells of pontine nuclei between fibers of pyramids, *d*, plexus of collaterals; *e*, descending collaterals.

band of white fibers which arches across the anterior aspect of the brain stem between the isthmus and the upper part of the medulla oblongata. This band contracts on each side into a rounded fiber mass, the *brachium pontis* or *middle cerebellar peduncle*, which arches upward to enter the cerebellum. The trigeminal nerve roots emerge between the fiber bundles of the base of the peduncle. The pons consists of a tegmental and a basilar part.

The *tegmentum of the pons* is the posterior portion which forms the floor of the fourth ventricle (Fig 151). Save for descriptive convenience there is

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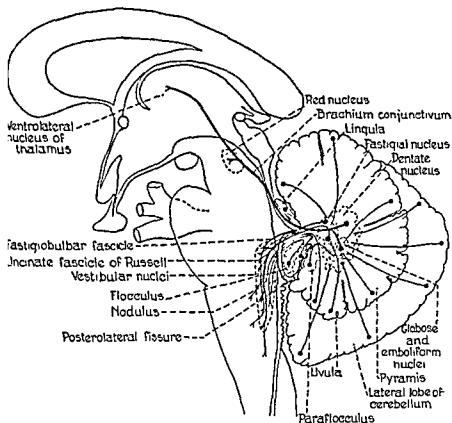


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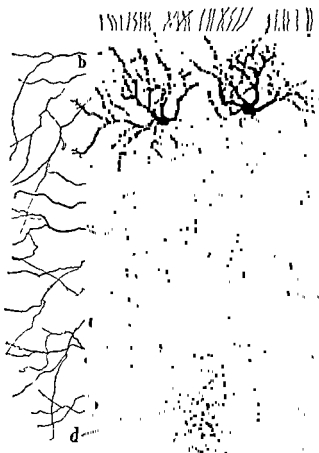


FIG. 150—CELLS AND FIBERS OF PONS OF KITTEN GOLGI METHOD. (From Cajal.)

a, collaterals from fibers of pyramids; *b*, other collaterals; *c*, cells of pontine nuclei between fibers of pyramids; *d*, plexus of collaterals; *e*, descending collaterals.

band of white fibers which arches across the anterior aspect of the brain stem between the isthmus and the upper part of the medulla oblongata. This band contracts on each side into a rounded fiber mass, the *brachium pontis* or *middle cerebellar peduncle*, which arches upward to enter the cerebellum. The trigeminal nerve roots emerge between the fiber bundles of the base of the peduncle. The pons consists of a tegmental and a basilar part.

The *tegmentum of the pons* is the posterior portion which forms the floor of the fourth ventricle (Fig. 151). Save for descriptive convenience there is

no special reason to differentiate it from the medulla oblongata. It is the portion of the rhombencephalon which has become enclosed, in phylogenetic development, by the great mass of fibers which connect the pontine nuclei with the cerebellum. It consists of a considerable zone of reticular formation, continuous with that of the medulla oblongata, below, and of the tegmentum of the midbrain above. The immediate floor of the ventricle in this region consists of a thick layer of gray substance with an ependymal covering. In addition the tegmentum contains the superior olivary nucleus and the trapezoid body. The *superior olive* is a secondary auditory nucleus and the *trapezoid body* is a great mass of auditory fibers which cross the midplane, forming the chief decussation

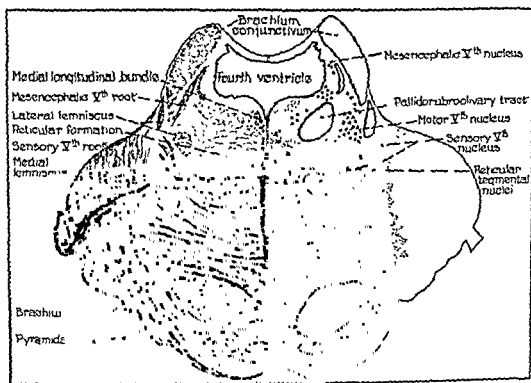


FIG. 1. CROSS SECTION THROUGH PONS AND CAUDAL PART OF MIDBRAIN.

of the auditory system. The remaining structures of the tegmentum are continuous with various nuclei and fiber bundles of the medulla oblongata below.

The *basilar part of the pons* is phylogenetically a new structure, quite distinct in development and connections from the tegmentum. It makes its appearance in the lower mammals, and its development is closely related to that of parts of the cerebral cortex and of the neocerebellum. There is evidence in lower mammals that the part of the pons caudal to the trigeminal roots receives fibers from the frontal lobe of the cerebrum, while the pretrigeminal part receives its fibers from the parietal lobe (Abbie). These fibers from the cerebral cortex have a longitudinal course and lie deep within the basilar part of the pons,

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forming large fascicles. Some of them end in the pontine nuclei, constituting the *corticopontine tract*, while others, the *corticobulbar* and *corticospinal tracts*, pass through the pons to emerge as the pyramids on the anterior side of the medulla oblongata.

Pontine nuclei.—The transverse or pons fibers proper lie superficially. They have their origin from masses of cells interspersed between the longitudinal and transverse fiber bundles. These cell masses are the pontine nuclei. They correspond to the arcuate nuclei of the medulla oblongata, but are much more developed in volume. The cells (Fig. 150) are of two types, namely, multipolar cells, which give rise to the brachium pontis fibers, and Golgi type II cells whose axons end within the pontine nuclei themselves and apparently serve as integrating neurons in the nuclei. In addition to the corticopontine tract already named, the pontine nuclei also receive collaterals from the pyramidal tracts which pass through the pons.

FUNCTION AND FUNCTIONAL LOCALIZATION IN THE CEREBELLUM

The cerebellum may be stated in general terms to be "the head ganglion of the proprioceptive system." To paraphrase Sherrington, it is the organ of a particular class of reactions which have their sources in receptor organs of several senses, but especially those whose functions have to do with space perception and those which serve proprioceptive stimuli. It also supports the tonus of most of the cranial and spinal nerve roots and plays an important part in the coordination of muscular action, both for maintenance of attitude and for carrying out of movements. It is concerned both with habitual posture and with movements, such as running and walking, which depend on the lower cerebral centers, as well as the skilled movements which depend on the cerebral cortex for control.

THE FLOCCULONODULAR LOBE—The results of recent experimental studies, coupled with clinical observations, indicate that the flocculonodular lobe is closely related, functionally, to the vestibular apparatus. The flocculus has its efferent connections directly with the vestibular nuclei (Dow, 1938). The nodulus likewise sends its fibers directly to the vestibular nuclei. The flocculonodular lobe thus has only vestibular connections, both afferent and efferent.

Lesions closely restricted to the nodulus and posterior part of the uvula, in macaques, resulted in marked disturbance of equilibrium, with oscillation of head and neck, ataxia of the trunk, falling, and staggering gait. There was, however, no tremor, hypotonia or disturbance of reflexes. Removal of the nodulus after destruction of the labyrinth on both sides produced no additional effect beyond a temporary increase in supporting reactions. In the chimpanzee similar results followed removal of the nodulus, without tremor, reduced muscle tone, or disturbance of reflexes. The experimental evidence amply justifies the

morphologic interpretation that the flocculonodular lobe is vestibular in its functional relationships.

The so-called posterior vermis syndrome of man is illuminated by this interpretation of the cerebellum, as Fulton and Dow (1937) have pointed out. Medulloblastoma of the nodulus produces disturbance of equilibrium and gait, without ataxia of the extremities or tremor so long as the patient is lying still (Bailey, 1933). These are vestibular symptoms. It should be recognized in this connection that the fact, pointed out by Ostertag (1936), that the nodulus is the last part of the cerebellum in which cellular differentiation ceases, embryologically, may fit into the pathological picture perfectly instead of being an apparently anomalous fact. The nodulus, while formed on the lateral commissure of the ancient auricular lobe, is itself a new structure, first appearing in mammals. If cessation of cell differentiation in the embryo has any relation to the phylogenetic age of any part of the brain, the nodulus should continue to differentiate cells long after many other cerebellar parts have ceased to do so.

CORPUS CEREBELLI.—The parts of the corpus cerebelli most closely related in position to the flocculonodular lobe, and representing the earliest outgrowths of the basis cerebelli, namely, the uvula and the lingula, receive both spinocerebellar and direct vestibular fibers. Both give efferents to the vestibular nuclei, as noted. The uvula also sends efferents to the fastigial nucleus. Whether or not the lingula also does so is not yet clear.

The *anterior lobe*, aside from the lingula, receives spinocerebellar fibers, both dorsal and ventral, and most of it receives secondary vestibular fibers. Its Purkinje cell axons pass to the fastigial nucleus. Dorsal spinocerebellar fibers pass to the lobulus simplex, the pyramis, paraslocculus and uvula of the posterior lobe. The uvula also receives secondary vestibular fibers, but the other parts named apparently do not. According to Ingvar the pyramis receives no direct vestibular fibers, although the older uvula does. The lobulus simplex, pyramis and uvula send efferents to the fastigial nucleus. The uvula alone, as already noted, sends efferents elsewhere in addition. The efferent connections of the fastigial nucleus are with the bulb and the cord through the uncinate bundle.

Little experimentation on the anterior lobe has been possible in monkeys. Removal of the lobe in the pigeon resulted in hypertonia and opisthotonus. Removal of one lateral half resulted in symptoms in the extremity of the opposite side. Complete destruction of the anterior lobe in the pigeon produced no visible effect on the vestibular reflexes.

In the decerebrate cat, extirpation of the anterior lobe of the corpus cerebelli was followed by increase in decerebrate rigidity. Removal of the entire cerebellum from a cat whose cerebral cortex had been removed on one side resulted in the hemiplegic extremity becoming rigid. This effect is referred by Fulton to the anterior lobe of the cerebellum.

Lesions of the *uvula* in monkeys produce a temporary effect on equilibrium, without involving any particular part of the body. Removal of the *pyramis* in

three monkeys resulted in inability to stop in time to avoid striking visible objects when the animal was running forward. This phenomenon is interpreted (Fulton and Dow, 1937) as due to some disturbance in distance perception. Electrical stimulation of the pyramis produces eye movements, as noted by Sherrington (1900), André-Thomas (1911) and Dow (1935). Fixation nystagmus appears to be related to lesions of the pyramis.

Trunk ataxia has been held due to injury to the posterior vermis, the trunk muscles having been assumed to be under control of the posterior vermis. Fulton holds however that the symptom is one of "disturbed coördination in space" and has nothing to do with localization of trunk muscles in the cerebellum. Dow has shown that these symptoms are due to injury to the flocculonodular lobe and are vestibular in origin.

Comparing the results of experimentation on the *nodulus*, *uvula* and *pyramis*, the so-called *posterior vermis* of many authors, it will be noted that these parts are functionally distinct. This is in keeping with their morphologic development and history. The *paraflocculus* is derived as a lateral extension of the uvula and the pyramis. It retains a peduncular connection with them, and its cortical association fibers, according to Jansen and Dow, are most closely related to uvula and pyramis. The efferent fibers of the paraflocculus, however, reach the zone of transition between nucleus interpositus and nucleus dentatus, with some ending in the dentate nucleus. No fibers, so far discovered, end in the fastigial nucleus. This gives the paraflocculus connections through the brachium conjunctivum rather than through the uncinate bundle. Its functional significance is obscure. No specific movements of the eyes or other parts have been observed in a restudy by Dow by stimulation of the paraflocculus. Certainly it has no relation to the flocculus, save connection by arcuate fibers, and the nystagmus movements formerly associated with it must be assigned to the flocculus. On the basis of comparative anatomy the tentative suggestion has been offered that it may have to do with proprioceptive impulses, other than vestibular, which play a part in maintaining equilibrium.

The *lobulus simplex* has been associated, functionally, with the neck muscles by van Rijnberk and others. There is no new evidence concerning this lobule.

NEOCEREBELLUM AND PALEOCEREBELLUM

It must be recognized that there are many stages in the evolution of the cerebellum. The first is represented by the commissure. This was followed by the cerebellar plate, corresponding to the basis cerebelli of mammals. With expansion of the cortex of the plate came folding, resulting in the main fissures of the corpus cerebelli. Also there is the stage, in reptiles, of differentiation of the *fars lateralis*, the forerunner of the ansiform lobule of mammals. In mammals, with the definite appearance of the pons and corticopontine-cerebellar connections, comes the medial lobe of Ingvar. There are no sharp boundaries between

these stages of development. Phylogenetically there is basis for a convenient division into *archicerebellum*, *paleocerebellum*, and *neocerebellum*. The boundaries, especially between *archicerebellum* and *paleocerebellum* are very vague, but, in general, the *archicerebellum* would include the *flocculi* and *basis cerebelli*, with part of the anterior lobe and possibly part of the posterior lobe of the *corpus cerebelli*. The *paleocerebellum* should include the major part of the anterior lobe, and the *uvula* and *pyramis* of the posterior lobe, with probably the attached *paraflocculus*. The term *neocerebellum* should be applied in a general way to the region receiving pontine fibers predominantly.

The emphasis on the *vermis* as a functional entity has been misleading. The *vermis* is made up of distinct units, some closely related to the ancient vestibular foundation of the cerebellum, others with spinal connections, and still others with the newer connections established by the higher brain centers. The *vermis* can be regarded as a separate division, even from the point of view of surface anatomy, only if the primate cerebellum, with its greatly hypertrophied ansiform lobule, is taken as the model form. The *vermis* belongs in part to *archicerebellum*, in part to *paleocerebellum*, and in part to *neocerebellum*.

Neocerebellum.—Bremer ablated the *neocerebellum* of cats and dogs on one side. The symptoms are described as homolateral, with the animal curving its body toward the side of the lesion. There is also a hypotonia, and volitional movements are accompanied by moderate tremor and hypermetria. These symptoms all disappear after two months unless the deep nuclei have been affected. There are no disturbances of equilibrium at any time.

Ablation of the *neocerebellum* in monkeys results in symptoms similar to those seen in cat and dog, with the addition of marked disturbance of skilled movements. In the baboon there is marked hypotonia. No tremor was noted save when the dentate nucleus was also involved. Unilateral and bilateral ablations of the *neocerebellum* were studied by Botterell and Fulton in monkeys and baboons. Unilateral ablation of the cortex alone results in transient hypotonia, awkwardness, and disturbance of gait on the same side. When the dentate nuclei were involved the symptoms named were more conspicuous and more lasting. There was also tremor in voluntary movement. Bilateral ablations of the cortex produced marked symptoms, with a disturbance of gait characterized by leaping and inability to arrest forward movement in face of an obstruction.

Botterell and Fulton have also studied the effects of such lesions on chimpanzees. The results were similar to those in monkeys but more enduring. There was extremely slow initiation of movements and marked hypotonia, the latter corresponding to that seen in man after *neocerebellar* injury from gunshot wounds.

The *tremor of cerebellar disease* is held by Walshe to represent imperfect compensation of other parts of the nervous system for cerebellar failure. Aring and Fulton found that removal of part of the frontal cerebral lobe anterior to the motor area, in monkeys, produced an exaggeration of cerebellar

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symptoms, and Fulton inferred that this area is responsible for cerebellar compensation. When voluntary movements are reduced by ablation of the motor area itself, there is decrease of cerebellar symptoms.

Cerebellar tremor does not occur from lesions of nodulus, uvula or pyramis, i.e., lesions of the so-called posterior vermis. Neither does it occur if, in addition, the fastigial nuclei are also removed. Ablation of the cerebellar cortex alone does not produce cerebellar tremor. If, however, the dentate or emboliform nuclei are involved tremor develops, but if part of the nuclei remains it disappears in part. If the brachium conjunctivum is severed, however, the tremor becomes permanent.

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CHAPTER 16

THE MIDBRAIN

The midbrain is a short segment connecting the pons and cerebellum with the forebrain (Fig. 152). In the embryo the neural plate rolls into a tube in this region. As development progresses the floor of the tube becomes thickened by development of nuclear masses and ingrowth of nerve fibers until it is much thicker than the roof. In the roof or tectum nuclear masses also develop, forming a *quadrigeminal plate*, so called from the two pairs of eminences seen from

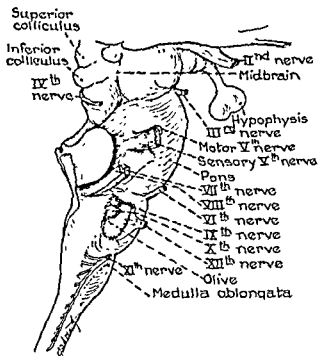


FIG 152—LATERAL VIEW OF BRAIN STEM.

above. The ventral part of the midbrain is called the *cerebral peduncle*. It is divided into the *basis pedunculi*, made up of descending fiber tracts, and the *tegmentum* which lies below the *ventricular cavity*. This cavity is called the *cerebral aqueduct* (*aqueduct of Sylvius*), and forms the connecting passage between the third and fourth ventricles.

THE TEGMENTUM.—A layer of gray matter, containing numerous pigmented cells, separates the basis pedunculi from the dorsally placed *tegmentum*. The teg-

THE MIDBRAIN

mentum is made up of mingled cells and fibers constituting the *reticular formation*, which is continuous with that of the medulla oblongata (Fig. 155). Some of these masses of cells in the tegmentum are sufficiently distinct to have individual names, but little is known of their individual functions. The most im-

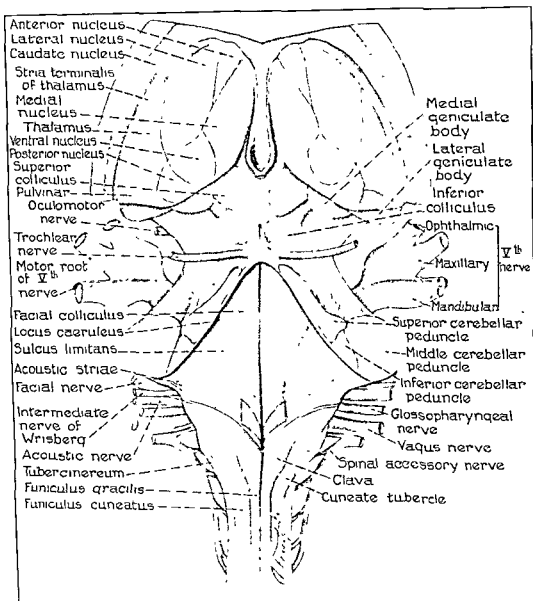


FIG 153—DORSAL VIEW OF BRAIN STEM

portant are the *dorsal* and the *ventral tegmental nuclei*, the *reticulotegmental nucleus*, the *superior central nucleus* and the *dorsal nucleus of the raphé*. The dorsal tegmental and the reticulotegmental cell groups receive fibers from the mammillary bodies indicating a relation to olfactory centers. The *reticulospinal* and *reticulobulbar tracts* are the principal efferent pathways.

The *red nucleus (nucleus ruber)* is the largest nuclear mass of the tegmentum.

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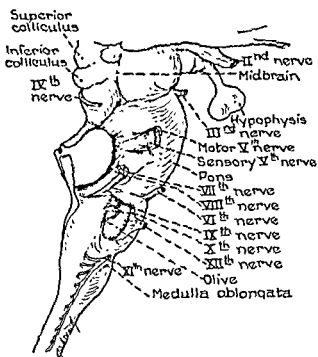


FIG 152—LATRAL VIEW OF BRAIN STEM.

above. The ventral part of the midbrain is called the *cerebral peduncle*. It is divided into the *basis pedunculi*, made up of descending fiber tracts, and the *tegmentum* which lies below the *ventricular cavity*. This cavity is called the *cerebral aqueduct* (*aqueduct of Sylvius*), and forms the connecting passage between the third and fourth ventricles.

The **TEGMENTUM**.—A layer of gray matter, containing numerous pigmented cells, separates the *basis pedunculi* from the dorsally placed *tegmentum*. The teg-

internal surface of the cerebral peduncle. The reticular zone is separated from the compact zone by a band of fibers, the *intermediate layer*. Its cells lie along the cerebral peduncle, and are more or less intermingled with the fibers of the latter.

The connections of the substantia nigra are not clearly understood in spite of much study. Ramón y Cajal describes collaterals to its nuclei from the motor fibers of the cerebral peduncle, i.e., *corticonigral fibers*. Other investigators have described direct fibers from the cortex, and still others have denied any such connection. Fibers from the medial lemniscus to these nuclei have also been claimed and denied. *Nigroreticular fibers* are recognized and nigroreticular fibers are probably present.

The *interstitial nucleus* of Ramón y Cajal is made up of scattered cells near the rostral end of the red nucleus and extending back along the medial longitudinal bundle. Their axons enter the bundle. A *ventral interstitial nucleus* has also been described.

The *nucleus of the medial longitudinal bundle* (*nucleus of Darkschewitsch*), also called the *nucleus of the posterior commissure*, lies dorsal to the interstitial nucleus. Its axons have been described as entering the medial longitudinal bundle of the same and the opposite side, reaching the latter through the posterior commissure.

The *interpeduncular nucleus* is one of the oldest, phylogenetically, in the vertebrate brain. It is an intermediate nucleus between the visceral and somatic olfactory centers of the diencephalon and the tegmentum of the midbrain. It is described by Ramón y Cajal in mammals as an unpaired mass consisting of a *superficial layer* and a *deep layer* of cells.

The cells of the outer layer vary in form, their dendrites being parallel to the brain surface. Their axons pass into the tegmentum. The deep layer is made up of small stellate cells and larger cells like those of the superficial layer. The axons of the small cells end in fine branches near the cell bodies (Golgi type II cells). The large cells send their axons into the tegmentum.

The *habenulopeduncular tract* (*fasciculus retroflexus* of Meynert) from the habenular nuclei, is the main afferent tract. There is also a *mammillopeduncular tract*. In amphibians the *nervus terminalis* appears to reach the interpeduncular nucleus.

The *pedunculotegmental tract* arises from this nucleus, passing to the dorsal tegmental nucleus. Impulses appear to be relayed through the medial longitudinal bundle to the motor nuclei of the midbrain and bulb.

The **QUADRIGEMINAL PLATE** (Fig. 153) is connected caudally to the cerebellum by the *anterior medullary velum*. This forms a thin roof of nervous substance above the rostral part of the fourth ventricle. The IVth nerve emerges from it. The upper or anterior two quadrigeminal bodies are called the *superior colliculi*. They are optic reflex centers, chiefly, and each receives a division, or so-called *root*, of the optic tract. The *posterior quadrigeminal bodies* or *inferior colliculi*

It is located medially about midway, in transverse sections (Fig. 156) between the basis pedunculi and the floor of the aqueduct of Sylvius. It extends rostrally into the ventral thalamus and caudally to the lower level of the inferior colliculus.

Microscopically the red nucleus consists of a group of large cells and a larger number of small cells, the two groups being fairly distinct. The large cells send dendritic processes in all directions, chiefly within the nucleus, and their axons cross and form the *rubrospinal tract*. The small cells form *rubro-reticular connections*, the impulses of which are probably relayed through the

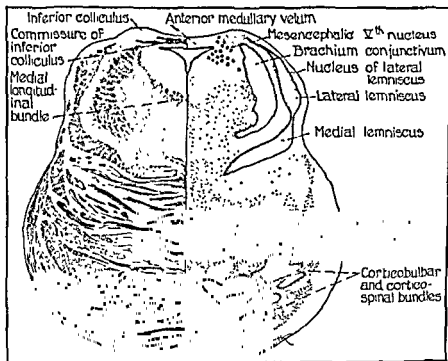


FIG. 154.—CROSS SECTION OF MIDBRAIN AT LEVEL OF INFERIOR COLICULUS AND PONS.

reticulospinal and other reticular pathways. *Rubrothalamic fibers* have also been described.

The principal fibers to the red nucleus are those of the brachium conjunctivum, from the dentate, globose and emboliform nuclei of the cerebellum. These fibers, with others, form a capsule medial to the nucleus. Most of the fibers of the brachium terminate within it, but Allen has clearly shown that a large number continue along its medial surface to end in the thalamus. *Corticorubral* fibers from the frontal lobe, *thalamorubral* and *incertorubral*, *striorubral* and *tectorubral* connections are also described.

The SUBSTANTIA NIGRA (Fig 156) is made up of cells of various sizes, small, medium and large. Foix and Nicolesco divide the cell groups in man into a *compact zone* and a *reticular zone*, a division confirmed in carnivores by Rioch. The compact zone extends from the pons to the mammillary bodies along the

of the inferior colliculus, and (3) a thin deep white layer, separating the nucleus from the aqueduct. The cells of the nucleus are large multipolar neurons with radiating dendrites. Their axons pass partly into the capsular layer and partly into the deep white layer. Those reaching the capsular layer enter the brachium of the medial geniculate body and probably reach the nucleus of the structure. Those entering the deep white layer pass into the tegmentum of the same and the opposite sides and descend. A few fibers of the deep white layer reach the opposite side by crossing above the aqueduct. There are also commissural fibers between the two nuclei.

The inferior colliculus receives, as its chief incoming fibers, the *lateral lemniscus* from the cochlear nuclei, superior olive and trapezoid body of the same and the opposite sides. It is the auditory reflex center. The lateral lemniscus fibers send branches to the medial geniculate body before entering the inferior colliculus. In most submammalian forms there are only two eminences on the dorsal surface of the midbrain. These correspond to the optic superior colliculi. In mammals, with their well developed, spirally wound cochlea, the inferior colliculi are added.

The efferent paths consist of a *tectospinal tract* which arises in part from the superior colliculus, a *tectopontine tract*, medial and lateral *tectonigral tracts* and a *tectobulbar tract*.

The *oculomotor* or *IIIrd nucleus* lies beneath the superior colliculus, ventral to the aqueduct of Sylvius and extends toward the third ventricle. The cells are arranged in groups variously described by different authors. In man Mingazzini divides the nucleus into paired *anterior dorsal*, *anterior ventral*, *posterior dorsal*, and *posterior ventral* subnuclei, in addition to a *medial nucleus*. The latter has been subdivided into a *central nucleus* of Perlia and a *central caudal nucleus*.

The lateral nuclei are made up of large multipolar cells. The central nuclei have smaller cells, but all appear to give rise to somatic motor fibers which constitute the greater part of the IIIrd nerve. The fibers pass through the tegmentum and red nucleus, many of them crossing, and emerge along the oculomotor sulcus on the anteromedial surface of the cerebral peduncle.

The fibers to the individual eye-muscles have been plotted, most recently by Brouwer, who agrees in general with the earlier results of Bernheimer. According to these results the main oculomotor nucleus supplies the muscles in order as follows, beginning rostrally: superior levator palpebrae, superior rectus, internal rectus, inferior oblique and inferior rectus. The central nuclei are regarded as involved in convergence of the eyes. Bernheimer states that the fibers to the inferior rectus all decussate, most of those to the inferior oblique cross, those to the internal rectus are chiefly uncrossed, and those for the superior rectus and superior levator of the eyelid are entirely homolateral. In addition to motor fibers, the IIIrd nerve contains proprioceptive fibers from neuromuscular and neurotendinous spindles in the eye muscles innervated by it.

receive fibers of the lateral lemniscus from the cochlear nuclei. They are chiefly auditory reflex centers.

The *superior colliculus* (Figs. 153 and 155) consists of a number of layers differing in histological pattern. Ramón y Cajal gives five layers. Kappers, Huber and Crosby list nine layers, which will be described briefly:

(1) The *superficial white layer* (*stratum zonale*) is a thin layer of fine fibers entering from the brachium of the superior colliculus. Among the fibers are scattered small to medium sized *tangential cells*. Some of the fibers enter the next layer.

(2) The *superficial gray layer* (*stratum griseum superficiale*) consists of numerous nerve cells of varying size. Small cells lie in the upper part of the layer, larger cells in the deeper part. All send their dendrites toward the superficial layer. Optic fibers from the third or optic layer end in relation to these cells.

(3) The *optic layer* (*stratum opticum*) consists of a few cells and many fibers, the latter being optic tract fibers which enter through the superior brachium.

(4) The *middle gray layer* (*stratum griseum mediale*) consists of cells whose axons form the fountain decussation of Forel and descend as the *tectospinal tract*.

(5) The *middle white layer* (*stratum album mediale*) is made up in part of axons from the fourth layer, and in part, of entering fibers from the spino-tectal tract.

(6) The *deep gray layer* (*stratum griseum profundum*) contains many cells of large size. Some of the axons pass into the tegmentum of the same side, others cross and reach the medulla oblongata and cord.

(7) The *deep white layer* (*stratum album profundum*) is made up of fibers from the above described cells.

(8) The *periventricular gray layer* (*stratum griseum periventriculare*) and

(9) The *periventricular white layer* (*stratum album periventriculare*) are intermingled. The fibers are largely tectobulbar and tectospinal.

The superior colliculus is regarded as entirely a reflex and correlation center for optic and tactile impulses. No fibers reach the cerebral cortex from this region but fibers from the occipital lobe reach the superior colliculus through the optic radiation.

The chief connections may be summarized as follows: *afferent fibers*, (1) through the optic tract from the retina; (2) through spino-tectal tract from the cord; (3) through optic radiation and superior brachium from the occipital lobe; *efferent fibers*, (1) through tectospinal tract; (2) through tectobulbar tract; (3) through tectopontile fibers; (4) collaterals from: (1) and (2) to the reticular formation and the red nucleus.

The *inferior colliculus* (Figs 153 and 154) microscopically shows (1) a superficial capsule of myelinated fibers; (2) a large mass of cells, the *nucleus*

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The *central gray matter of the aqueduct* is continuous with the gray matter of the fourth ventricle. In the midbrain it is 2 to 3 mm. thick. The part dorsal to the aqueduct has numerous small nerve cells. Larger cells continue upward from the *locus caeruleus* of the fourth ventricle. In the opossum these are obviously mesencephalic Vth cells, a chain of which continues from the mesencephalic Vth nucleus of the midbrain to the point of emergence of the Vth roots. In man there are also groups of cells connected with the IIIrd and IVth roots. The fibers of the central gray form a fine network and just beneath the ependyma numerous fine, longitudinal fibers are present.

DECUSSATIONS IN THE MIDBRAIN.—In addition to the decussations of the IIIrd and IVth nerves there is the *ventral tegmental decussation* or *decussa-*

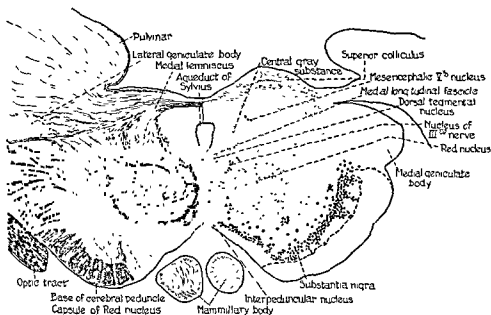


FIG 156.—CROSS SECTION THROUGH THE ROSTRAL PART OF THE MIDBRAIN, AND THE MEDIAL GENICULATE BODIES.

tion of Forel, made up of fibers from the red nuclei which descend, after crossing, as the rubrospinal tract. The *dorsal tegmental decussation* is made up of fibers from the superior colliculi which descend, after crossing, as the *tectobulbar* and *tectospinal* tracts. The *decussation of the brachium conjunctivum* forms a large mass of fibers crossing the midplane below the inferior colliculus. The superior and inferior colliculi are also joined across the midplane to their fellows by commissural fibers.

The **BASIS PEDUNCULI** (Figs. 155 and 156) is composed of the great mass of descending fibers from the cerebral cortex to the pons, bulb and cord. These fibers emerge from the internal capsule of the forebrain and continue over the anterior surface of the substantia nigra. They form bilateral masses which converge toward the pons and pass beneath the masses of pontile fibers.

The *nucleus of Edinger-Westphal* (Fig. 153) lies rostral to the main oculomotor nucleus, near the midplane. It consists of a vertically arranged medial mass and a horizontally spread lateral mass of cells. The cells are small and give rise to small myelinated preganglionic fibers which emerge with the IIIrd nerve to reach the ciliary ganglion. Postganglionic fibers from this ganglion reach the ciliary muscle of the eye and the constrictor fibers of the iris.

The nucleus of Edinger-Westphal is included in the visceral efferent group. It receives fibers from the pretectal region which have to do with light reflexes

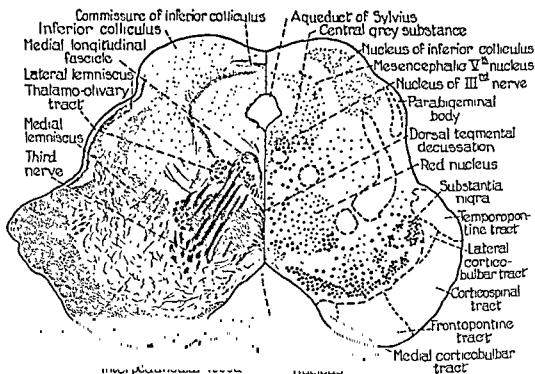


FIG. 155—CROSS SECTION THROUGH MIDBRAIN AND CEREBRAL PEDUNCLE AT LEVEL OF THE SUPERIOR COLICULUS.

of the eye. Stimuli from this nucleus produce contraction of the pupil and accommodation of vision on the same side.

The *trochlear or IVth nucleus* (Fig. 153) consists of large multipolar cells which form a group in the gray layer anterior to the aqueduct, at the level of the inferior colliculus. Fibers from these cells pass somewhat caudally around the central gray and decussate in the anterior medullary velum. It is usually stated that decussation is complete, but Van Gehuchten describes a few fibers as not crossing. The nerve emerges from the roof of the anterior velum and reaches the superior oblique muscle. In addition to motor fibers there are proprioceptor fibers to neuromuscular spindles in this muscle. In the rabbit Weinberg found cells of the mesencephalic Vth type among the motor cells of the IVth nucleus.

THE MIDBRAIN

the IIIrd nerve roots on the side of the lesion. The loss of sensation on the opposite side is due to involvement of the medial, spinal and trigeminal lemniscus systems above their levels of decussation. The muscular effects in the extremities are due to involvement of the red nucleus.

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A TEXTBOOK OF NEURO-ANATOMY AND THE SENSE ORGANS

In transverse section the basis pedunculi is somewhat crescentic in outline. Fiber bundles from various parts of the cortex occupy distinct positions. The fibers from the cortex to the medulla oblongata are divided into a *medial corticobulbar tract*, located at the medial margin of the crescent, and a *lateral corticobulbar tract*, located in the deep portion of the lateral part of the peduncular base. The *temporopontile tract*, from the temporal lobe, occupies the lateralmost portion, and the *corticospinal tract* occupies the middle three-fifths of the peduncle. The *frontopontile tract*, from the frontal lobe to the pons, occupies the ventral medial part of the peduncle.

In addition to the large bundles named there are several aberrant tracts regarding which there is much confusion. The *lateral pontine bundle* of Marburg has been variously regarded as an aberrant pyramidal bundle, as part of an extrapyramidal system, etc. Included in the pes pedunculi, fibers from the globus pallidus to the substantia nigra (*pallidonigral tract*) and also *pallido-tegmental* fibers have been described.

In addition to the basis pedunculi, other fiber systems pass through the midbrain. The largest of these is the medial lemniscus from the bulb to the thalamus. The *lateral lemniscus*, from the cochlear centers of the bulb, partly ends in the inferior colliculus, but in part passes on to the medial geniculate body of the thalamus. In connection with the upper part of the bulbothalamic tract are found the *spinothalamic tracts* and *central sensory 1st tract*. *Thalamo-olivary fibers* descend dorsomedially to the red nucleus, and the *median longitudinal bundle* lies below the central gray matter near the midplane.

CLINICAL INTERPRETATION

SOME LESIONS OF THE MIDBRAIN

CEREBRAL PEDUNCLE SYNDROME (WEBER'S SYNDROME).—Lesions in the lower and internal side of the cerebral peduncle may produce external deviation of one eye, with drooping of the eyelid (ptosis), loss of accommodation and of the light reflex; spastic paralysis of the extremities of the opposite side; facial and hypoglossal paralysis of the opposite side. The ocular symptoms are due to involvement of the roots of the IIIrd nerve on the side of the lesion. The paralysis of the extremities, facial muscles and tongue is due to involvement of the corticospinal and corticobulbar fibers above their level of decussation.

ALTERNATING PARALYSIS OF THE IIIrd NERVE, WITH SENSORY PARALYSIS AND MUSCULAR TREMOR (BENEDIKT'S SYNDROME).—Lesions of the midbrain may involve one side of the tegmentum in such a manner as to produce external deviation of one eye, with ptosis, double vision, loss of accommodation and light reflexes, loss of cutaneous sensibility of body and face on the opposite side; tremor and irregular, spasmodic involuntary movements of the limbs of the opposite side (hemichorea). The ocular symptoms are due to involvement of

thalamus and cerebral hemispheres. The structures developed from the visceral sensory region become the hypothalamus. It contains olfactory and gustatory centers and centers of correlation of visceral impulses. It is also intimately connected structurally and functionally with the hypophysis, one of the most important of the glands of internal secretion.

EPITHALAMUS

The epithalamus includes the *habenular trigone*, the *medullary stria of the thalamus*, the *posterior commissure*, and the *pineal body*. It forms the dorsal-most part of the diencephalon.

The HABENULAR TRIGONE is a depressed triangular area rostral to the superior colliculus. It contains a *medial* and a *lateral habenular nucleus* on each side, the two together forming a fusiform mass. The size of the habenulae is in proportion to the degree of development of the olfactory apparatus in various animals, being larger in macrosmatic animals. They are connected by the *habenular commissure*.

The medullary stria is made up of fibers from various olfactory centers, including the cortex of the hippocampus. These all reach the habenular nuclei. It also contains fibers to and from the tectum of the midbrain. Some of the fibers of the stria cross in the posterior commissure to the contralateral nuclei.

The *habenulo-interpeduncular tract* or the *fasciculus retroflexus* of Meynert constitutes the principal outgoing connection of the habenulae. It arises chiefly from the medial nucleus and passes to the interpeduncular nucleus.

The habenular region is the diencephalic center for somatic olfactory stimuli. Here such impulses are correlated with other somatic sensory stimuli, especially those relayed from the tectal region.

The PINEAL BODY OR EPIPHYSIS is considered by many students of the brain as a vestigial organ related to the parietal eye of lower vertebrates. Others regard it as a gland of internal secretion. Experimental studies have given contradictory results.

In man the pineal body is a cone-shaped structure 5 to 8 mm. long and about 4 mm. in diameter. It lies in the hollow between the superior colliculi, and under the splenium of the corpus callosum. It is separated from the latter by the tela chorioidea of the third ventricle. It is attached by a stalk which divides into a dorsal and a ventral layer. The *dorsal lamina* is continuous with the habenular commissure. The *ventral lamina* is continuous with the posterior commissure. Between the two lies the *pineal recess* of the third ventricle, lined with ependyma.

Embryologically the epiphysis is an ependymal outgrowth from the roof of the betweenbrain. The cells at the apex proliferate and differentiate into neuroglia and parenchyma. The parenchyma cells become arranged into cord-like lobules. They develop numerous processes which either are lost in the

CHAPTER 17

THE DIENCEPHALON

The diencephalon or betweenbrain is formed by the constriction of the forebrain vesicle into two secondary subdivisions. It lies between the telencephalon and the midbrain. In the adult stage (Fig. 157) it includes (1) the *epithalamus* (pineal body, habenulae, medullary striae of the thalamus, and posterior commissure); (2) the *thalamus* (dorsal thalamus, medial and lateral geniculate bodies); (3) the *ventral thalamus* or *subthalamus*; (4) the *hypothalamus* (tuber cinereum, mammillary bodies, and posterior lobe of hypophysis).

Its cavity, the *third ventricle*, extends forward somewhat into the telencephalon, but the greater part is a vertical cleft between the two halves of the diencephalon. The ventricle is covered above by a layer of ependyma attached to the *tectia thalami* on each side. Above the ependyma lies a layer of pia mater, the *tela chorioidea*, from which vascular folds extend into the ventricle as its *chorioid plexus*. Rostrally the ventricle is bounded by the *lamina terminalis* which, morphologically, is the anterior end of the forebrain vesicle. It forms a thin plate from the optic chiasma to the anterior commissure. Above the commissure it is continuous with the rostrum of the corpus callosum. Between the lamina terminalis and the optic chiasma there is a ventral pocket of the ventricle known as the *optic recess*.

The floor of the ventricle is formed by the *optic chiasma*, the *infundibulum*, the *subthalamus* and the *mammillary bodies*. The lateral walls, from below upwards, are formed by *hypothalamus*, *subthalamus* and *thalamus*, together constituting the medial surface of the entire diencephalon. Near the rostral end the ventricle opens on each side into the lateral ventricles. The communications are known as the *interventricular foramina* or *foramina of Monro*. Caudally the third ventricle continues into the cerebral aqueduct.

The rostral terminus of the sulcus limitans, which divides the basal or motor plate of the neural tube from the alar or sensory plate, has an important bearing on interpretation of diencephalic structures. According to Kingsbury and Johnston the limiting sulcus ends at the mammillary recess. The basal plate therefore terminates at this point also, if this interpretation be accepted. The alar plate extends around the mammillary recess and gives rise to all the structures derived from the forebrain vesicle. These all would be continuations of the sensory column, the motor column ending at the mammillary recess.

The ventral, visceral sensory portion extends to a point just rostral to the infundibular recess. The more dorsal, somatic sensory structures include the

THE DIENCEPHALON

Nageotte as secretory granules. After the age of puberty deposits of calcium salts are common in the epiphysis, usually in the neuroglia cells. According to Bailey such deposits are rare before the age of fourteen. The supposed function of the pineal body as an organ of internal secretion has been studied by various investigators, but with inconclusive results. It has been thought by some to be related to the onset of puberty.

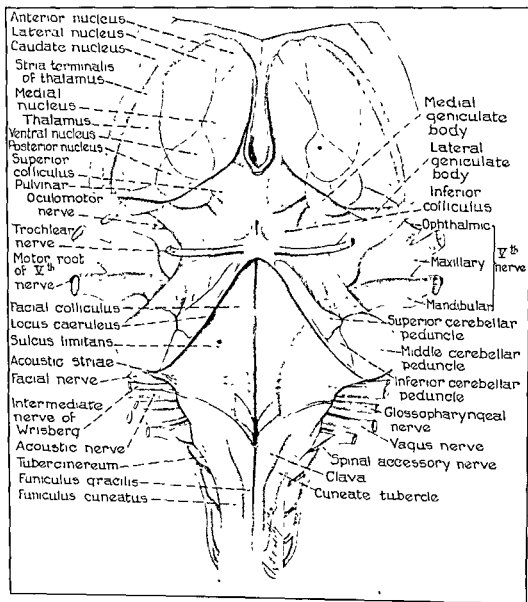


FIG 158—DORSAL VIEW OF BRAIN STEM.

THE THALAMUS

The human thalamus (Figs 158 and 159) is a complex mass of nuclei and fibrous connections. Before describing it a brief account of the fundamental

interior of the lobule or end in bulbous enlargements near the connective tissue septa. The cytoplasm is relatively small in amount. Rio del Horta described granules in these cells which he considered as secretory. Some of the cells are

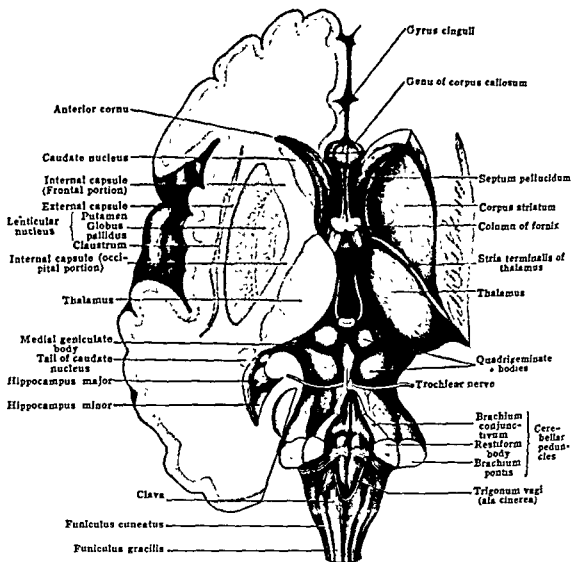


FIG 157—HORIZONTAL DISSECTION SHOWING GRAY AND WHITE SUBSTANCE OF TELENCEPHALON BELOW THE CORPUS CALLOSUM AND THE RELATIVE POSITION OF THE DIENCEPHALON.

From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co, Philadelphia, 1933. after Landois and Stirling.

pale and some stain deeply by Horta's special methods. The nuclei of all the cell types are pale.

The neuroglia cells are numerous near the peduncles and pineal recess. They are scattered through the parenchyma and are distinguished from the parenchyma cells by their smaller and darker nuclei and their generally fibrous processes. The neuroglia cells contain numerous gliosomes which are regarded by

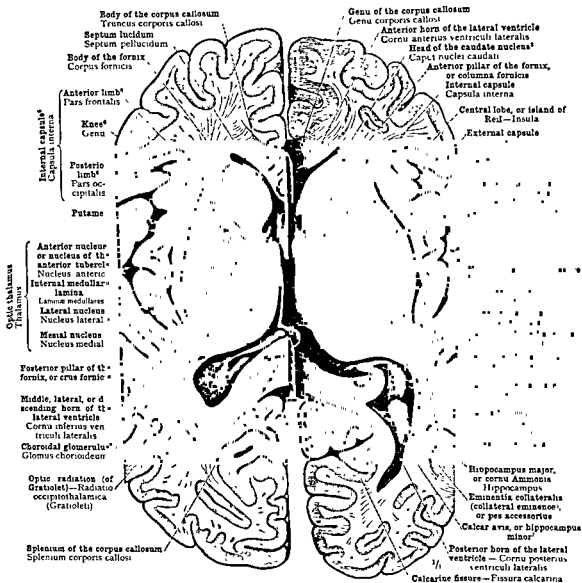


FIG 159—HORIZONTAL SECTION OF CEREBRAL HEMISPHERE THROUGH THALAMUS AND STRIATUM

From Toldt, *Atlas of Anatomy*,

pattern as it exists in urodeles will be given. Herrick divides the thalamus in Necturus, into *dorsal* and *ventral* parts, the ventral being the larger. In its subsequent evolutionary development the dorsal thalamus has expanded into many sensory nuclei and the ventral thalamus has become reduced to the subthalamus of mammals which is a motor coördinating center.

In urodeles the *dorsal thalamus* is a primitive somatic sensory correlation center. It receives (1) optic fibers from the retina; (2) cutaneous sense and proprioceptive fibers from the medulla oblongata and cord; (3) some olfactory fibers from the stria medullaris; and (4) fibers from the tectum of the mid-brain. The latter carry impulses already integrated from tactile, proprioceptive, visual and cochlear stimuli which reach the midbrain directly.

In higher vertebrates the dorsal thalamus becomes differentiated into distinct nuclear masses, some of these, e.g., the lateral and medial geniculate bodies, receiving direct stimuli from the end organ (retina) or from the primary center. Others receive stimuli already integrated.

The *ventral thalamus* in urodeles is a somatic motor adjustor apparatus receiving somatic sensory impulses of all sorts from higher centers of correlation. Its efferent impulses are regarded as concerned with mass movements and total reactions of the body.

THALAMIC NUCLEI

The *thalamic nuclei* in man may be divided into three groups, namely, (1) *nuclei with subcortical connections*, i.e., the *nuclei of the midline*, the *intralaminar nuclei*, the *centromedian nucleus* of Luys, and the *anterior ventral nucleus*; (2) *cortical relay nuclei*, including the *lateral ventral*, *posterior ventral* and the *anterior nuclei*, together with the geniculate bodies; (3) *association nuclei*, including the *dorsomedial*, *posterior lateral* and *dorsal lateral nuclei*, and the *pulvinar*.

NUCLEI OF PALEOTHALAMUS.—The first group has no connections with the cerebral cortex. The *nuclei of the midline* are designated the *paleothalamus*. Their connections are with the supra-optic nuclei of the hypothalamus and the pretectal nuclei. Their functions are probably visceral. The *intralaminar* and the *centromedian nuclei* are regarded as concerned with intrathalamic associations, but the centromedian nucleus has connections with the globus pallidus. The anterior ventral nucleus is not affected by removal of the cerebral cortex but its connections and function are unknown.

The **CORTICAL RELAY NUCLEI**, save the anterior, receive the ascending sensory fibers of the spinal, medial, lateral and trigeminal lemniscus systems and of the optic tracts. Together with the association nuclei they constitute the *neothalamus*. The ascending somatic sensory fibers, including general cutaneous and deep sensibility (pain, temperature, touch, pressure, proprioceptive sense, etc.) are called collectively the *somaesthetic group*.

The *anterior nuclei*, consisting of *dorsal anterior*, *ventral anterior* and *medial*

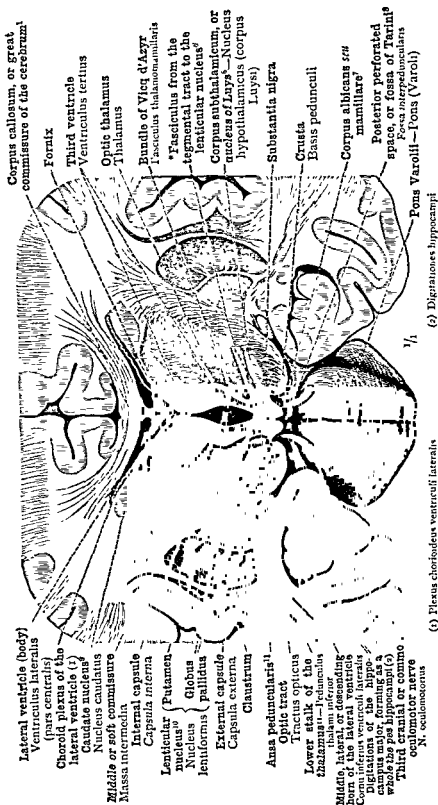


FIG. 160—CORONAL SECTION OF CEREBRAL HEMISPHERE THROUGH DIENCEPHALON AT LEVEL OF MAMMILLARY BODIES.

From Tolbt, *Atlas of Anatomy*, The Macmillan Co., New York, 1926.

anterior, receive fibers from the mammillary bodies through the bundle of Vic d'Azyr. They give rise to projection fibers to the cortex of the base of the frontal lobe and of the gyrus cinguli. They are functionally related to the olfactory system.

The *lateral ventral nucleus* receives most of the thalamic fibers of the brachium conjunctivum. These have their origin in the dentate nucleus of the cerebellum. Projection fibers reach the lateral frontal lobe, save the area of the arcuate sulcus. They relay unconscious proprioceptive impulses from the cerebellum to the motor areas of the cortex. Experimental lesions in parts of the frontal lobe (areas 4 and 6) of monkeys, to which these fibers project, were followed by delayed reaction, or complete loss of reaction when the affected limbs, paralyzed by the lesions, were placed in abnormal positions. According to Dusser de Bar  nne there is a topographical representation, in the nucleus, of the cortical areas of foot, arm and face. Lesions of the motor face area produced degeneration in the medial region of the nucleus, while lesions of arm and foot areas produced degeneration in the intermediate and lateral parts, respectively, of the nucleus.

The *posterior ventral nucleus* receives the spinothalamic, trigeminal and medial lemniscus systems. Projection fibers pass from it to the primary somatic sensory cortex found chiefly in the postcentral gyrus. The trigeminal lemniscus ends in the medial part of the nucleus. From this region projection fibers pass to the region of the operculum, forming the sensory cortical area for the face. The intermediate part of the nucleus sends projection fibers to the sensory arm and trunk areas of the cortex, while the lateralmost part projects to the leg area. The rostral part of the nucleus sends its fibers to the deep part of the fissure of Rolando, and the more posterior part sends fibers to the surface of the post-central gyrus.

The *medial geniculate body* is an expansion of the region of the dorsal thalamus which receives the lateral lemniscus. Malone describes a *dorsal* and a *ventral* nucleus in man. In addition to the lateral lemniscus the medial geniculate body receives fibers from the inferior colliculus through the brachium of this colliculus. Its chief efferent fibers take their course from the auditory radiations to the superior temporal gyrus, reaching the cortex through that part of the posterior limb of the internal capsule which passes beneath the lenticular nucleus. The medial geniculate bodies of the two sides are connected together by the commissure of Gudden. This is a bundle of fibers which arches ventrally in association with the optic tract on each side and crosses the midplane in the posterior part of the optic chiasma. Gudden's commissure, as it separates from the optic tract to enter the medial geniculate body, forms the so-called medial root of the optic tract.

The *lateral geniculate body* is the primary optic center of the thalamus, receiving fibers directly from the retina. According to von Monakow 80 per cent of the retinal fibers terminate in the center. It is made up of six layers of

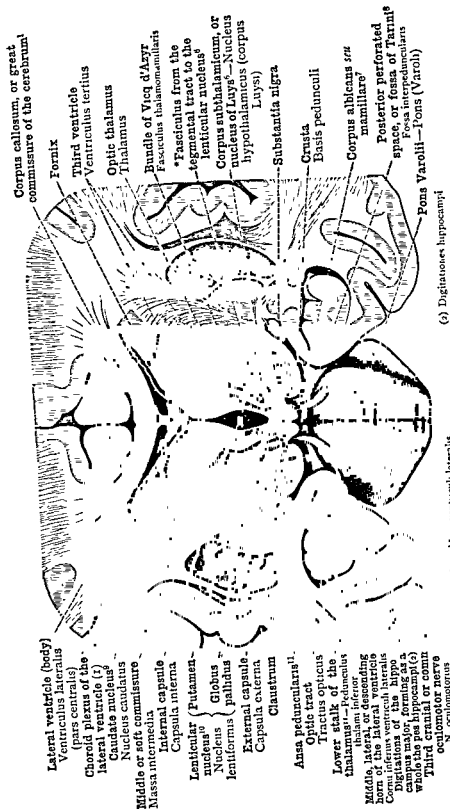


Fig 160—CORONAL SECTION OF CEREBRAL HEMISPHERE THROUGH DIENCEPHALON AT
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From Toldt, *Atlas of Anatomy*, The Macmillan Co, New York, 1926.

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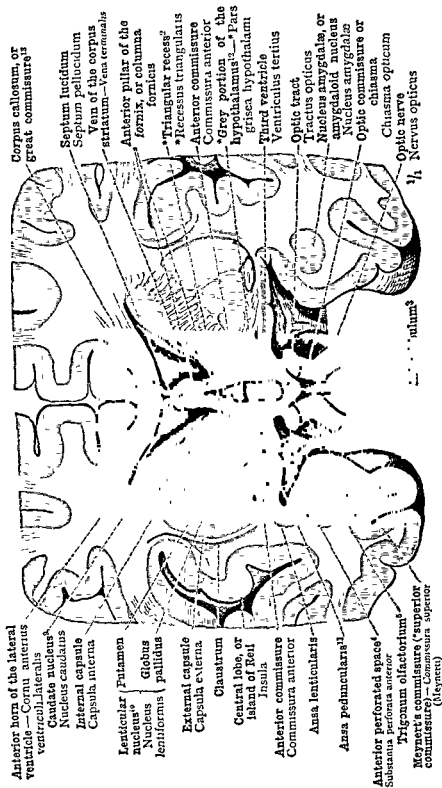


FIG. 161.—CORONAL SECTION BEHIND THE OPTIC COMMISSURE OR CHIASMA, PASSING THROUGH THE INFUNDIBULUM AND THE ANTERIOR PILLAR OF THE FORNIX OR COLUMNÆ FORNICIS, POSTERIOR SURFACE OF ANTERIOR SEGMENT

A view is obtained of the interior horns of the lateral ventricles; the anterior wall of the third ventricle is displayed. (From Toldt, *Atlas of Anatomy*.) By permission of The Macmillan Company, publishers.

cells with fiber layers between. Minkowski pointed out that crossed and uncrossed retinal fibers enter alternate layers. This has been confirmed in man by MacKenzie. In lower primates a large nucleus which can be differentiated into *dorsal* and *ventral* portions has been described. The dorsal nucleus is the chief terminus and relay station for the optic fibers. In man this nucleus is well differentiated, but a ventral part has not been recognized.

Projection of the Retina.—Studies by means of lesions in the retina have shown that there are definite zones in the lateral geniculate body receiving fibers from specific parts of the retina. Brouwer and Zeeman found, in monkeys, that "the dorsal half of the peripheral retina is projected medially in the external geniculate body and the lower half laterally." They further concluded, from their comparative studies on rabbits, cats and monkeys, that the greater part of the dorsal nucleus is concerned with binocular vision. Fibers from the macula reach the central portion of the dorsal nucleus. Macular fibers and fibers from the periphery of the retina overlap in the ventral part of the nucleus, but elsewhere the peripheral fibers are distinct, in their distribution, from the macular fibers. In man the centers for macular vision and peripheral retinal localization, as described by Roune, agree in general with the results above described. Henschen describes a sharper localization of retinal areas in the lateral geniculate nucleus than is indicated by the results of Brouwer and Zeeman.

In addition to the optic tract the lateral geniculate body receives fibers from the pulvinar and from the superior colliculus. It gives off the *optic radiations* to the occipital lobe, fibers to the superior colliculus through the brachium of the lateral geniculate body, and fibers to neighboring nuclei.

The ASSOCIATION NUCLEI do not receive fibers from the ascending tracts but have connections with the nuclei which receive these fibers, on the one hand, and with the cerebral cortex on the other. Their projection fibers pass to the association areas of the cortex, however, in contrast to the cortical fibers of the relay nuclei which end in cortical projection areas.

The *medial dorsal nucleus* is connected with the lateral thalamic nuclei. It has a large celled portion, connected with hypothalamic nuclei and a small celled portion connected with the prefrontal association area of the cortex. Experimental evidence suggests that this nucleus plays a part in association of sensory data from the other nuclei of the thalamus and possibly from the hypothalamus.

The *lateral posterior nucleus* is closely connected with the ventral posterior nucleus, probably serving as a relay station as well as an association center for the ventral posterior nucleus. Le Gros Clark regards it as a nucleus concerned with the integration of incoming sensory impulses and with transmitting the partially integrated impulses to the cerebral cortex. Its efferent fibers end in the parietal lobe, save the postcentral gyrus.

The *pulvinar* is an outgrowth of the lateral posterior nucleus which has appeared late in evolutionary development. It consists of lateral, medial and inferior divisions. It has connections with the posterior ventral nucleus, in which

THE DIENCEPHALON

The fields H_1 and H_2 of Forel, better called the *reticular subthalamic nuclei* of Papez and Rioch, are mixed white and gray substance. The main fiber bundles are the continuation of part of the brachium conjunctivum beyond the red nucleus to its destination in the thalamus. There is also the lenticular bundle of Forel. According to Kappers, Huber and Crosby, the main nuclei of the subthalamus chiefly are way stations interposed in the course of the *ansa lenticularis* for discharge of impulses from the corpus striatum to the lower centers. It is regarded as part of the somatic coördinating system and as forming the main path for discharge of the corpus striatum.

THE HYPOTHALAMUS

The *hypothalamus* is the ventral subdivision of the betweenbrain (Figs. 162 and 163). It includes the *optic chiasma*, the *infundibulum*, the *hypophysis*, the

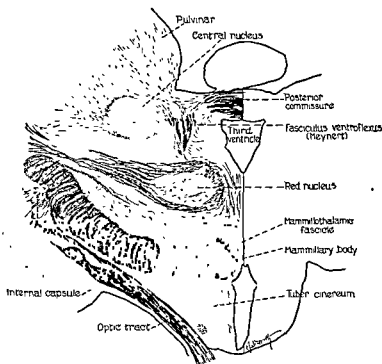


FIG 162—TRANSVERSE SECTION THROUGH THALAMUS AND HYPOTHALAMUS

tuber cinereum and the *mammillary bodies*. These structures form the greater part of the floor of the third ventricle.

The *optic chiasma* is formed chiefly of the optic fibers, part of which decussate. There is included also the commissure of Gudden between the medial geniculate bodies. Rostral to the chiasma, lying between it and the lamina terminalis, there is a *preoptic recess* whose lateral and rostral boundaries belong to the telencephalon.

The *tuber cinereum* is a rounded eminence of gray substance between the optic

end the lemniscus systems, but connections with the geniculate bodies and the colliculi have not been established. The inferior part sends fibers to the cortex of the occipital lobe and receives fibers from this part of the cortex. The medial part projects to the region of the auditory cortex. Brouwer considers the pulvinar as a center for controlling movements of the eye muscles and having to do with recognition of relative and absolute distance, and with stereoscopic vision. Fulton believes it has a part in visual and auditory integrations.

Corticothalamic Fibers.—Various parts of the thalamus receive projection fibers from the cortex. Brouwer (1932) has suggested that through these connections the cortex may bring about a "sensory attention" to incoming impulses to the thalamic nuclei. Such corticothalamic fibers have been described as follows: (1) from the striate area of the occipital lobe to the lateral geniculate body; (2) from the auditory cortex of the temporal lobe to the medial geniculate body; (3) from the parietal lobe to the lateral nucleus; (4) from the precentral gyrus (area 4) to the anterior part of the lateral and ventral nuclei; (5) from area 19 to the pulvinar, and to the lateral and ventral nuclei of the thalamus; (6) from a small area of the cortex in front of the motor face area (frontal eye fields) and the prefrontal cortex to the dorsomedial nucleus. It will be noted that, in general, these fibers pass from the region of cortex to which a given thalamic nucleus projects its fibers, back into that nucleus. An interplay of impulses between cortex and nuclei is made possible by this arrangement.

SUBTHALAMUS

The *subthalamus* or *ventral thalamus* lies ventral to the medial sulcus of the diencephalon. Kappers, Huber and Crosby describe it as the forward continuation of the midbrain tegmentum. It consists of several nuclei and numerous fibers.

The *subthalamic nucleus* or *body of Luys* lies just rostral to the substantia nigra, above the cerebral peduncle. Its chief connections are with the corpus striatum by a striosubthalamic bundle, and with the contralateral red nucleus. Thalamosubthalamic fibers and corticosubthalamic fibers are also described. Efferent fibers constitute a subthalamonigral tract.

The *entopeduncular nucleus* is placed in the course of the ansa lenticularis, a fiber bundle between the pes pedunculi and the lentiform nucleus. The cells, which resemble those of the globus pallidus save that they are smaller, are described as surrounded by pericellular baskets from fibers of the ansa. They are of motor type.

The *zona incerta* lies between the peduncle and the subthalamic nucleus. It receives fibers from the ansa lenticularis. There are connections with the lateral geniculate body and with the nucleus ruber. This region is regarded as a zone through which fibers pass from higher to lower centers, and as a relay station in the path of the ansa lenticularis.

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The *fields H₁ and H₂ of Forel*, better called the *reticular subthalamic nuclei* of Papez and Rioch, are mixed white and gray substance. The main fiber bundles are the continuation of part of the brachium conjunctivum beyond the red nucleus to its destination in the thalamus. There is also the lenticular bundle of Forel. According to Kappers, Huber and Crosby, the main nuclei of the subthalamus chiefly are way stations interposed in the course of the *ansa lenticularis* for discharge of impulses from the corpus striatum to the lower centers. It is regarded as part of the somatic coordinating system and as forming the main path for discharge of the corpus striatum.

THE HYPOTHALAMUS

The *hypothalamus* is the ventral subdivision of the betweenbrain (Figs. 162 and 163). It includes the *optic chiasma*, the *infundibulum*, the *hypophysis*, the

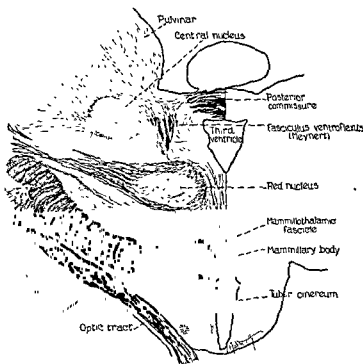


FIG. 162—TRANSVERSE SECTION THROUGH THALAMUS AND HYPOTHALAMUS

tuber cinereum and the *mammillary bodies*. These structures form the greater part of the floor of the third ventricle.

The *optic chiasma* is formed chiefly of the optic fibers, part of which decussate. There is included also the commissure of Gudden between the medial geniculate bodies. Rostral to the chiasma, lying between it and the lamina terminalis, there is a *preoptic recess* whose lateral and rostral boundaries belong to the telencephalon.

The *tuber cinereum* is a rounded eminence of gray substance between the optic

chiasma and the mammillary bodies. It continues on each side to the anterior perforated substance, and rostrally to the lamina terminalis.

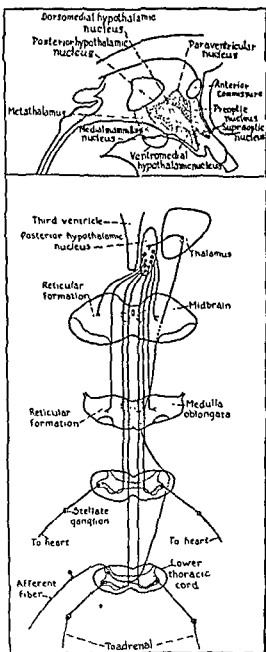


FIG 163.—DIAGRAM OF HYPOTHALAMIC NUCLEI AND SOME CONNECTIONS.

After Le Gros Clark and Beattie, Brown and Long.

The *infundibulum* is a funnel-like process from the tuber cinereum which projects downward and somewhat rostrally to the hypophysis. It is continuous with the posterior lobe of this organ, forming its stalk.

The *hypophysis* is a gland of internal secretion having a double origin embryologically. The anterior lobe is derived from Rathke's pocket of the pharyngeal cavity. The posterior lobe is derived from the floor of the third ventricle.

The *mammillary bodies* are two elevations, one on each side of the midline, just rostral to the posterior perforated substance. Externally they are white because of a capsule of myelinated fibers. Internally each shows a *lateral* and a *medial* nucleus. The mammillary bodies receive the numerous fibers of the *fornix* which connects them to olfactory centers. They give rise to the *mammillothalamic tract* or *bundle of Vicq d'Azyr*.

HYPOTHALAMIC NUCLEI

The human hypothalamus is divided into four regions, according to Le Gros Clark, each with its group of nuclei, totaling 15 to 20 in number. The four regions or areas are more marked in the four months' foetus, but are recognizable in the adult. Above and rostral to the optic chiasma lies the *supra-optic part*, behind the chiasma is the *infundibular part*, and the caudal extremity of the hypothalamus is formed by the *mammillary part*.

The *pars supra-opticus* contains the *paraventricular* and the *supra-optic nucleus*. The paraventricular nucleus consists of large, closely packed cells. It extends rostrally to the anterior commissure,

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above to the rostral extremity of the hypothalamic sulcus, and below to a point 3 mm. above the optic chiasma. It is a large, flattened group of cells lying close to the ventricular lining. The *supra-optic nucleus* is made up of closely packed cells extending from the lateral margin of the optic chiasma toward the mammillary body. It shows two groups of cells, the *laterodorsal* and *ventromedial supra-optic nuclei* of Gagel. The supra-optic nucleus is connected with the paraventricular by a chain of small cell groups and by a fiber tract (Greving). Colloidal cell inclusions have been reported by Scharer in this and the paraventricular nucleus, which he regards as evidence of secretory activity by the cells. In lower verte-

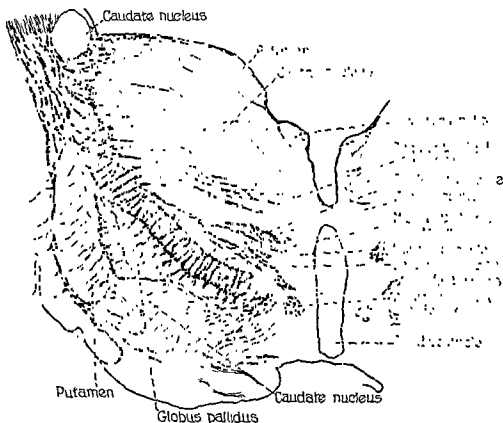


FIG 164—TRANSVERSE SECTION THROUGH THALAMUS AND CAUDAL PART OF STRIATE BODY

brates the paraventricular and supra-optic nuclei are represented by the *preoptic nucleus*, extending from the optic chiasma to the wall of the preoptic recess.

The *fars infundibularis* contains three nuclei. The *ventromedial nucleus* consists of small, rounded or oval cells crowded together. It is located between the supra-optic nucleus, rostrally, and the posterior hypothalamic nucleus, caudally, differing from both in cell structure. The *dorsomedial nucleus* is distinguished from the ventromedial by less crowding of cells and less sharp delimitation. It lies near the ventricular surface of the hypothalamus, extending to the hypothalamic sulcus. The *lateral hypothalamic area* is a region lateral to the plane of the fornix made up of small, scattered groups of large cells. The cells are

separated from the ventromedial nucleus of the supra-optic area by a zone of small cells. Laterally they extend to the margin of the tuber cinereum and above they are continuous with the *nucleus perifornicalis* around the fornix. This area is larger and more distinct in the human brain than in other primates. In the superficial part of this area, in man, there are well defined groups of small cells called the *nuclei tuberis*, surrounded by layers of fibers. Outside of these fiber capsules lie the large cells of the lateral area. The *nuclei tuberis* consist of a *medial* and a *lateral* group. Their significance is unknown but they appear to be absent in lower mammals.

The *retro-infundibular part* of the hypothalamus includes the *posterior nucleus*. It consists of single or small groups of large, oval cells scattered in a dense matrix of small cells. Ventrally the large cells are arranged somewhat in rows curving upward and backward. Dorsally the cells are more irregular in arrangement. The posterior nucleus appears to give rise to the majority of the periventricular fibers and appears to be an efferent nucleus for impulses from hypothalamus to the brain stem and cord.

The *mammillary part* of the hypothalamus has three nuclear masses, namely, the *medial*, the *lateral*, and the *intercalated* mammillary nuclei. The *medial nucleus* is a large, homogeneous mass of small cells, sharply marked off from surrounding structures by a thin capsule of myelinated fibers. It is connected with the anteroventral nucleus of the thalamus by the bundle of Vicq D'Azyr, this entire system being relatively more highly developed in man than in other mammals. Le Gros Clark regards this system, namely, medial mammillary nucleus, mammillothalamic tract and ventral anterior nucleus of thalamus, which in turn projects to the gyrus cinguli of the cerebral cortex, as the route through which impulses from the hypothalamus may be carried to the neopallium. The *lateral mammillary nucleus* is small. It is composed of small, compactly arranged cells and lies against the lateral convex surface of the medial nucleus. It is reduced in higher primates and man, as compared with lower mammals. The *intercalated nucleus* is made up of large cells similar to those in the lateral hypothalamic area. It invests the lateral nucleus laterally and ventrally. Crouch states it is only found in primates and should not be confused, because of its position, with the lateral nucleus above described. The descending fornix fibers terminate in all three nuclei of the mammillary body, although the mammillothalamic fibers arise from the medial nucleus above.

FUNCTIONS OF THE HYPOTHALAMUS

Dogs from which the cerebral cortex is removed retain their autonomic reflexes, but animals decerebrated by section of the brain stem in front of the pons lose them. With both cerebral hemispheres removed, but with the brain stem and hypothalamus intact, the animals are subject to periods of sham rage (Cannon and Bard). This condition is characterized by dilatation of the pupils,



FIG. 165.—CORONAL SECTION PASSING THROUGH THE ANTERIOR PORTION OF THE PONS VAROLII, THE OPTIC THALAMI AND THE POSTERIOR EXTREMITY OF THE LENTICULAR NUCLEUS, ANTERIOR SURFACE OF THE POSTERIOR SEGMENT. The central portion of body and the middle, lateral, or descending horn of the lateral ventricle. (From Toldt, *Atlas of Anatomy*) By permission of The Macmillan Company, publishers.

separated from the ventromedial nucleus of the supra-optic area by a zone of small cells. Laterally they extend to the margin of the tuber cinereum and above they are continuous with the *nucleus perifornicalis* around the fornix. This area is larger and more distinct in the human brain than in other primates. In the superficial part of this area, in man, there are well defined groups of small cells called the *nuclei tuberis*, surrounded by layers of fibers. Outside of these fiber capsules lie the large cells of the lateral area. The *nuclei tuberis* consist of a *medial* and a *lateral* group. Their significance is unknown but they appear to be absent in lower mammals.

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(4) reduced intragastric pressure; (5) complete loss of gastro-intestinal peristalsis, not affected by section of the vagi; (6) movements of the extremities; (7) vasoconstriction; (8) increased metabolic activity; (9) increased heat production; (10) diffuse discharge in all divisions of the thoracolumbar autonomic system. Lesions of this nucleus cause: (1) reduced metabolic rate; (2) fall in body temperature due to peripheral dilatation, panting, sweating and reduced metabolic activity. Large bilateral lesions are followed by Horner's syndrome, i.e., relaxed nictitating membrane, drooping of eyelids, extreme contraction of pupils and abnormal sinking of eyes into the orbit. All of these symptoms are also produced by section or paralysis of the cervical sympathetic trunk. With unilateral lesions of the posterior hypothalamic nucleus the syndrome is slight.

The *mammillary bodies* have important olfactory connections, but stimulation has been said to produce sleep, and destruction causes somnolence and catalepsy both in cats and monkeys (Ranson). Hess holds that a center governing the various muscular and other phenomena associated with sleep is located between the posterior hypothalamic nucleus and the oculomotor nucleus. Le Gros Clark regards sleep as due to a reduction of hypothalamic activity, accompanied by reduction of hypophyseal function also.

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HYPOPHYSIS

The *hypophysis* or *pituitary body* is a gland of internal secretion. It consists of an *anterior lobe* or *pars buccalis* and a *posterior lobe* or *pars nervosa* as its two principal divisions. The anterior lobe is derived from the ectodermal Rathke's

increased heart rate and blood pressure, erection of hairs, salivation, etc. All the symptoms enumerated are due to discharges through the sympathetic system. Bard was able to prove that the posterior hypothalamic nuclei are involved in such manifestations. Other sympathetic symptoms, such as extra systoles of the heart beat in thalamic animals, have been traced to the posterior hypothalamic region. These were abolished by cutting the ventral roots of the nerves supplying sympathetic fibers to the heart, by cutting the medial longitudinal bundle or by removing the stellate ganglion, all indicating a sympathetic pathway for the impulses responsible (Beattie, Brow and Long).

A great deal of attention has been given in recent years to the function of specific hypothalamic regions and nuclei. Stimulation and destruction of various parts have given supplementary data which may be summarized briefly, using Le Gros Clark's four regions as a basis.

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The *paraventricular nucleus* appears to be concerned with carbohydrate metabolism. Destruction of this nucleus is followed by permanent deficiency of sugar in the urine (hypoglycemia). The experimental animals also have an abnormal sensitivity to insulin.

The *ventromedial hypothalamic nucleus* (medial part of tuber cinereum) and *dorsomedial hypothalamic nucleus* (dorsal nucleus of tuber cinereum) on stimulation show (1) reduced heart rate, (2) increased intragastric pressure, (3) increased peristalsis, (4) increased bladder tonus. The cardiac and gastro-intestinal effects are stopped by section of the vagus nerves. The bladder effect is stopped by section of the sacral autonomic branches or by injection of atropin.

Experimental lesions of these nuclei have resulted in (1) hemorrhagic erosions of the gastric mucosa; (2) the adiposogenital syndrome, characterized by a gradual fat deposition, genital atrophy, and a tendency toward the feminine body type; and (3) are said to prevent onset of experimental diabetes after removal of the pancreas.

The *lateral hypothalamic area* or lateral part of the tuber cinereum has given, on stimulation, (1) complete inhibition of gastro-intestinal peristalsis; (2) increased respiratory rate (panting); (3) increased blood pressure; (4) dilatation of pupil (Ectors, 1937).

The *posterior hypothalamic nucleus*, when stimulated, produces: (1) increased heart rate; (2) dilated pupils; (3) increased rate of respiration (panting);

(4) reduced intragastric pressure; (5) complete loss of gastro-intestinal peristalsis, not affected by section of the vagi; (6) movements of the extremities; (7) vasoconstriction; (8) increased metabolic activity; (9) increased heat production; (10) diffuse discharge in all divisions of the thoracolumbar autonomic system. Lesions of this nucleus cause: (1) reduced metabolic rate; (2) fall in body temperature due to peripheral dilatation, panting, sweating and reduced metabolic activity. Large bilateral lesions are followed by Horner's syndrome, i.e., relaxed nictitating membrane, drooping of eyelids, extreme contraction of pupils and abnormal sinking of eyes into the orbit. All of these symptoms are also produced by section or paralysis of the cervical sympathetic trunk. With unilateral lesions of the posterior hypothalamic nucleus the syndrome is slight.

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CHAPTER 18

THE CEREBRAL HEMISPHERES

The telencephalon is made up of the *cerebral hemispheres*, the *corpus striatum* and the region just rostral to the optic chiasma known as the *pars optica hypothalami*. The anterior part of the third ventricle extends into the telencephalon. The cavities of the cerebral hemispheres, known as the *lateral ventricles* communicate with the third ventricle through the interventricular foramen (foramen of Monro) on each side. In man the cerebral hemispheres completely cover the brain stem and the cerebellum, making these parts invisible from above.

The TELEENCEPHALON is derived from the more anterior of the two brain segments formed by constriction of the embryonic forebrain vesicle. In the embryo of about one month there begins an evagination on each side which becomes the anlage of the hemispheres. The upper part becomes the *pallium*. In the floor there occurs a thickening, especially pronounced laterally, which becomes the *corpus striatum*. At first this is continuous with the corresponding thickening in the betweenbrain, the thalamus. Presently it is separated by a groove.

The plate between the hemispheres grows at a slower rate, with the result that a deep furrow is formed, representing the *sagittal fissure*. The rostroventral continuation of this plate, which is the morphological anterior end of the forebrain, becomes the *lamina terminalis*. The hemispheres grow rostrally beyond this plate on each side. Ventral to the pallium of each hemisphere there appears a swelling which elongates in the rostrocaudal axis, and becomes the olfactory lobe. It is the beginning of the rhinencephalon.

By the fifth month (Fig. 167) of fetal development a distinct lobation of the hemispheres into *frontal*, *parietal*, *temporal* and *occipital* lobes is apparent. Between the frontal, parietal and temporal lobes a flattened area appears during the third month. With growth of the lobes this becomes depressed below the general cerebral surface. It is continuous internally with the mass of the corpus striatum, the area representing the developing cortex above the striate body. This *insula* or *island of Reil* becomes covered as development of the cortex continues, by overgrowth from all sides by the margins of the lobes surrounding it. These margins become the *opercula* of the insula, named from their respective lobes as operculum of frontal lobe, etc. A fissure in the adult, known as the *lateral fissure* (*fissure of Sylvius*) opens to the hidden cortical surface of the island of Reil.

pocket. The posterior lobe, embryologically, is a hollow evagination of the diencephalic floor which retains a connection with the brain by the infundibular stalk. The cavity of the lobe disappears in man by thickening of its walls.

The *posterior lobe* is made up of mossy neuroglia cells and large multipolar cells resembling nerve cells, but without Nissl substance. Herring bodies, variously interpreted by different investigators, are also found in the posterior lobe. They have been regarded as colloidal masses, as degenerated cells, and as a special type of nerve fiber termination. Ranson has demonstrated a bundle of nerve fibers from the supra-optic nucleus to the posterior lobe and pars intermedia. Cushing holds that the posterior lobe produces a secretion which is discharged through the infundibular stalk into the third ventricle. This suggests a functional relation to the nervous system.

The *anterior lobe* produces several secretions, the description of which belongs to the domain of endocrinology. A *pars intermedia* and a *pars tuberalis*, both derived from the pars buccalis, produce endocrine secretions which have specific functions differing from those of the anterior lobe proper.

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CHAPTER 18

THE CEREBRAL HEMISPHERES

The telencephalon is made up of the *cerebral hemispheres*, the *corpus striatum* and the region just rostral to the optic chiasma known as the *pars optica hypothalami*. The anterior part of the third ventricle extends into the telencephalon. The cavities of the cerebral hemispheres, known as the *lateral ventricles* communicate with the third ventricle through the interventricular foramen (foramen of Monro) on each side. In man the cerebral hemispheres completely cover the brain stem and the cerebellum, making these parts invisible from above.

The TELECEPHALON is derived from the more anterior of the two brain segments formed by constriction of the embryonic forebrain vesicle. In the embryo of about one month there begins an evagination on each side which becomes the anlage of the hemispheres. The upper part becomes the *pallium*. In the floor there occurs a thickening, especially pronounced laterally, which becomes the *corpus striatum*. At first this is continuous with the corresponding thickening in the betweenbrain, the thalamus. Presently it is separated by a groove.

The plate between the hemispheres grows at a slower rate, with the result that a deep furrow is formed, representing the *sagittal fissure*. The rostroventral continuation of this plate, which is the morphological anterior end of the forebrain, becomes the *lamina terminalis*. The hemispheres grow rostrally beyond this plate on each side. Ventral to the pallium of each hemisphere there appears a swelling which elongates in the rostrocaudal axis, and becomes the olfactory lobe. It is the beginning of the rhinencephalon.

By the fifth month (Fig. 167) of fetal development a distinct lobation of the hemispheres into *frontal*, *parietal*, *temporal* and *occipital* lobes is apparent. Between the frontal, parietal and temporal lobes a flattened area appears during the third month. With growth of the lobes this becomes depressed below the general cerebral surface. It is continuous internally with the mass of the corpus striatum, the area representing the developing cortex above the striate body. This *insula* or *island of Reil* becomes covered as development of the cortex continues, by overgrowth from all sides by the margins of the lobes surrounding it. These margins become the *opercula* of the insula, named from their respective lobes as operculum of frontal lobe, etc. A fissure in the adult, known as the *lateral fissure* (*fissure of Sylvius*) opens to the hidden cortical surface of the island of Reil.

pocket. The posterior lobe, embryologically, is a hollow evagination of the diencephalic floor which retains a connection with the brain by the infundibular stalk. The cavity of the lobe disappears in man by thickening of its walls.

The *posterior lobe* is made up of mossy neuroglia cells and large multipolar cells resembling nerve cells, but without Nissl substance. Herring bodies, variously interpreted by different investigators, are also found in the posterior lobe. They have been regarded as colloidal masses, as degenerated cells, and as a special type of nerve fiber termination. Ranson has demonstrated a bundle of nerve fibers from the supra-optic nucleus to the posterior lobe and pars intermedia. Cushing holds that the posterior lobe produces a secretion which is discharged through the infundibular stalk into the third ventricle. This suggests a functional relation to the nervous system.

The *anterior lobe* produces several secretions, the description of which belongs to the domain of endocrinology. A *pars intermedia* and a *pars tuberalis*, both derived from the pars buccalis, produce endocrine secretions which have specific functions differing from those of the anterior lobe proper.

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Flechsig has shown that myelinization takes place in various parts of the nervous system and in specific tracts at various stages in the embryo, beginning at about four months. In the cerebral hemispheres it begins at about the time of birth and continues until puberty. The four primary groups of projection fibers, namely, olfactory, visual, acoustic and somæsthetic, are the first affected. The areas whose fibers connect primary cortical areas with thalamic and pontine nuclei are myelinated next in order. Finally the association fibers such as those of the corpus callosum, etc., receive their myelin sheaths.

The sagittal fissure of the embryonic brain becomes filled with mesenchyme which condenses into the sickle-shaped *falx cerebri* of the dura mater. The falx extends downward to the corpus callosum, arching in front and behind the latter so as to completely separate the hemispheres save in the middle region. The anterior end of the corpus callosum curves downward and tapers, in sagittal

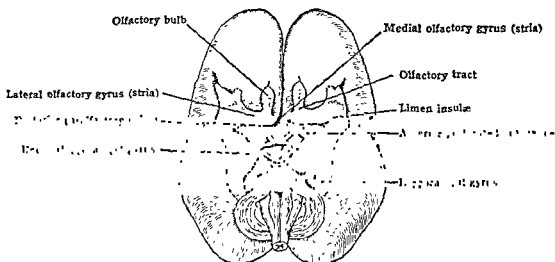


FIG. 167.—VENTRAL VIEW OF BRAIN OF FIVE MONTHS' FOETUS.

(From Retzius)

section, to join the lamina terminalis. The curved part of the callosum is called the *genu*, the tapering part is the *rostrum*. The posterior end of the corpus callosum is thickened into the *splenium*, which lies above the midbrain.

The dorsal surface of the part of the corpus callosum between the hemispheres is covered by a thin layer of gray matter, the *indusium griseum*. It is marked by two longitudinal bands of fibers on each side of the midline, known as the *medial longitudinal stria (stria Lancisii)* and the *lateral longitudinal stria*, respectively. They are composed of fibers connecting olfactory areas, and the *indusium griseum* is, in man, a reduced part of the olfactory cortex.

A white band, called the *fornix*, arches from the underside of the *splenium* to the anterior commissure. In the roughly triangular area between *fornix* and the arch of the corpus callosum the medial wall of the hemisphere is formed by a thin layer of cortex known as the *septum pellucidum*. The medial surfaces of the septa of the two hemispheres, covered by *meninges*, are in contact save for

The wall of the hemispheres begins to thicken in the third month of development. This process begins in the basal parts near the striate body and extends over the pallium. Differentiation into zones of cells and fibers also begins. From the fourth month onward the wall thickens rapidly, largely because of the great increase in fibers in the intermediate zone which pass from the basal ganglia to the cortex. Presently fibers from cortical cells are added to the mass, resulting in the white substance of the hemisphere. The ventricle becomes reduced, as a result, from a large space to a narrow slit.

The white matter continues to increase in volume, but the cortical gray matter spreads out in a thin layer. This however folds into numerous *gyri* separated by furrows known as *sulci* or *fissures*. Many of the folds correspond, in general,

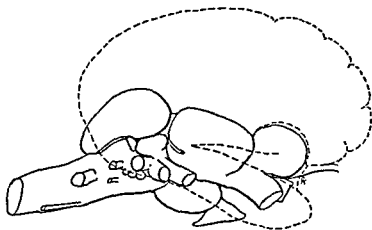


FIG. 166—DIAGRAM OF BASAL GANGLIA AND RELATION TO CORTEX.

(After Edinger.)

to histological areas of the cortex, these in turn representing functional areas in some cases.

The first fissures to appear are the *hippocampal* and the *rhinal*. These mark off the primitive olfactory system from other parts of the brain. They may be recognized during the third month, when the fissure of Sylvius also makes its appearance. During the fifth month the *calcarine*, *parieto-occipital* and *central* fissures appear, marking off distinct areas of the cortex. During the sixth and seventh months the other main fissures appear as shallow grooves. These are the *inferior* and *superior precentral*, the *postcentral*, the *superior temporal*, the *parolfactory*, the *superior* and *inferior frontal*, the *interparietal*, the *callosomarginal* and the *orbital* fissures. The calcarine and the hippocampal fissures produce elevations within the ventricle. Transitory fissures have been described during the third and fourth months but are now regarded as artefacts.

The primary fissures named are located, in general, in the regions of the primary functional areas of the cortex. Association areas are formed between and around them, which, as they expand, give rise to secondary gyri. These may greatly modify the form and position of the primary gyri.

THE CEREBRAL HEMISPHERES

lobe forms the posterior part of the hemisphere. It is bounded on its lateral surface by the parieto-occipital fissure and by a line continued from the end of

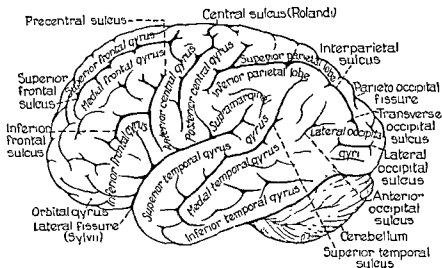


FIG. 169.—LATERAL VIEW OF BRAIN

this fissure to the pre-occipital notch. Its medial surface is bounded from the parietal lobe by the medial part of the parieto-occipital fissure. The central lobe

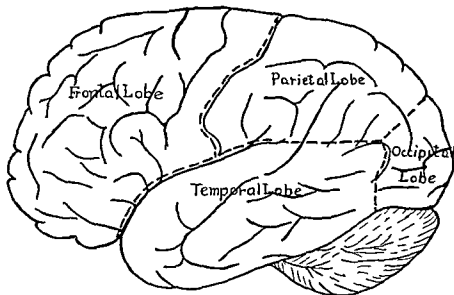


FIG. 170.—DIAGRAM OF LOBES OF CEREBRUM

or insula is covered by the opercula which are separated from each other by the fissure of Sylvius and the anterior and posterior ram of this fissure.

THE BASAL GANGLIA

The floor and ventrolateral wall of the cerebral hemisphere contains several masses of gray substance beneath the cortex (Fig. 166). They include the

a cavity of variable size known as the *cavum septi* or fifth ventricle. This is, of course, merely a meningeal space.

The adult cerebral hemisphere (Figs. 168-171) is divided into six lobes as follows: *frontal lobe*, *parietal lobe*, *temporal lobe*, *insula* or *central lobe* (*island of Reil*), *occipital lobe*, and *olfactory brain* or *rhinencephalon*, which includes

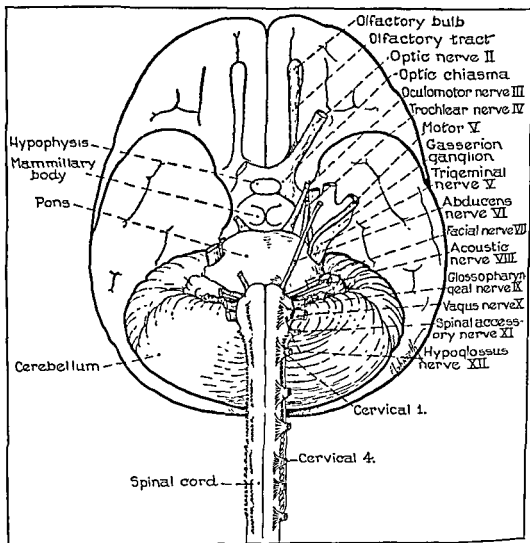


FIG. 168—VENTRAL VIEW OF ADULT BRAIN.

structures in other lobes. The *frontal lobe* is bounded posteriorly by the central fissure, the fissure of Sylvius and an arbitrary line between the posterior limb of the latter and the lowest part of the central fissure. The *parietal lobe* lies between the central fissure anteriorly, and the parieto-occipital and lateral occipital fissures posteriorly. A line from the tip of the Sylvian fissure extended to the lateral occipital fissure separates the parietal and temporal lobes. The *temporal lobe* lies between the Sylvian fissure and the parieto-occipital. The *occipital*

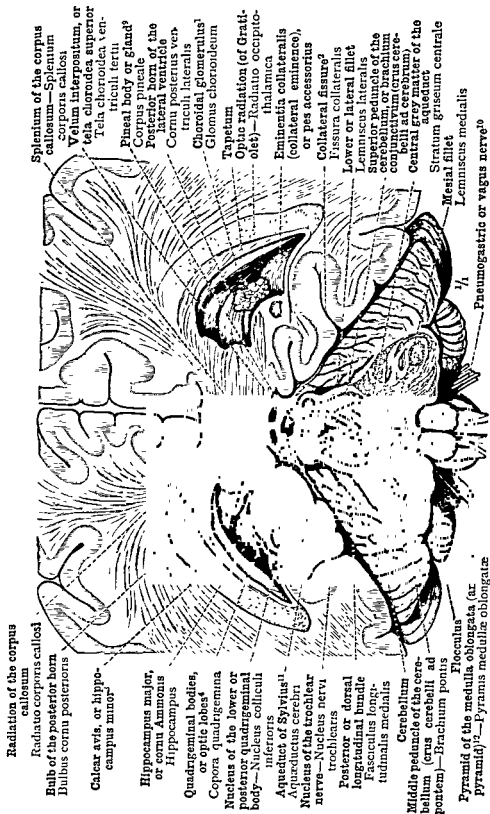


FIG. 172.—CORONAL SECTION PASSING BEHIND THE PONS VAROLII THROUGH THE UPPER EXTREMITIES OF THE PYRAMIDS AND THROUGH THE SPLENIUM OF THE CORPUS CALLOSUM, ANTERIOR SURFACE OF POSTERIOR SEGMENT.

A view is obtained into the posterior horns of the lateral ventricles (From Toldt, *Atlas of Anatomy*.) By permission of The Macmillan Company, Publishers.

striate body, the amygdaloid nucleus and the claustrum, and collectively are known as the basal ganglia (Figs. 172-174). The anterior limb of the internal capsule passes through the mass, separating the greater part of the caudate nucleus from the lenticular nucleus of the striate body. The posterior limb of the internal capsule separates the lentiform nucleus from the thalamus. The external capsule, a thin sheet of white substance, lies between the lateral surface of the lentiform nucleus and the claustrum. Between the claustrum and the cortex of the insula there is another band of white known as the *capsula extrema*. Bands of gray matter connect the caudate and lentiform nuclei through

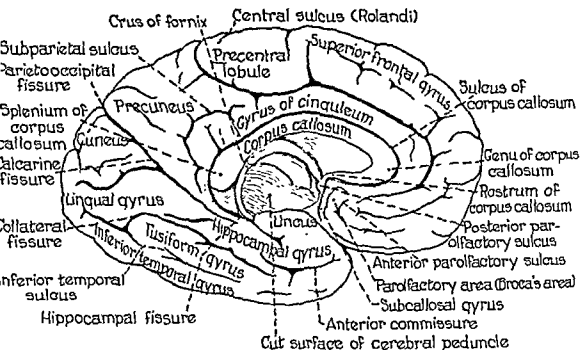


FIG. 171.—MEDIAL SECTION OF ADULT BRAIN.

the internal capsule and bands of white fibers are numerous in the lentiform nucleus. In section these bands of gray and white have a striated appearance from which the mass derives its name.

The **CLAUSTRUM** is a thin layer of gray substance usually regarded as a detached portion of the cortex of the insula. However, it comes to the surface at the anterior perforated substance and is continuous with the gray matter of the cerebral cortex. It is made up of small, spindle-shaped cells similar to those in the deepest layer of the cortex.

The **AMYGDALOID NUCLEUS** lies at the lateral extremity of the anterior perforated substance in front of and partly above the tip of the inferior horn of the lateral ventricle. It is continuous with the cortex of the pyriform lobe. Phylogenetically it is derived from the olfactory telencephalon. The most caudal part of the cortex fold

triatum, which

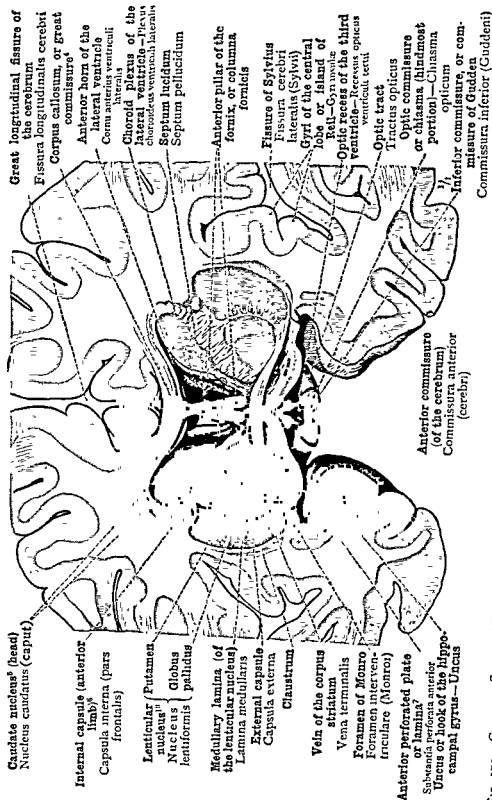


FIG. 173.—CORONAL SECTION PASSING THROUGH THE OPTIC COMMISSURE OR CHIASSMA AND THROUGH THE ANTERIOR COMMISSURE OF THE CEREBRUM, ANTERIOR SURFACE OF POSTERIOR SEGMENT.

A view is obtained into the third ventricle from before. (From Todd, *Atlas of Anatomy*.) By permission of The Macmillan Company, publishers.

Kappers regards as homologous with the mammalian amygdaloid mass. It is regarded as a center of correlation of olfactory with somatic impressions. It gives rise, in large part, to the *stria terminalis*, a band of fibers which arches with the caudate nucleus to reach the region of the anterior perforated substance. This is the chief efferent tract. Other connections of the amygdaloid complex are with the cortex of the pyriform lobe, the septum pellucidum and the lateral olfactory tract.

The **STRIATE BODY** (**CORPUS STRIATUM**) lies in the floor and lateral wall of the lateral ventricle in front of the thalamus. The gray substance is made up of the *caudate nucleus* and the *lentiform nucleus*. The anterior limb of the internal capsule passes between the greater part of these two nuclei, but they are joined in front of the capsule.

The *caudate nucleus* is divided into the *head*, which projects into the lateral ventricle, and the *tail* or *cauda*. The cauda arches over the thalamus and passes forward under this mass to end in the region of the amygdaloid nucleus. The head of the caudate nucleus is continuous with the anterior perforated substance, as well as with the lentiform nucleus, as stated.

The *lentiform nucleus* is buried in the white substance of the hemisphere. It is subdivided by the *external* and *internal medullary stria* into three masses. The two medial masses are yellowish in color. Together they are somewhat spherical and form the *globus pallidus*. The lateral mass is larger and has a reddish color in the fresh brain. It is called the *putamen*.

The *globus pallidus* is the older part of the striate body, constituting the *paleostriatum*. It is more or less continuous with the endopeduncular nucleus of the diencephalon. It is made up of small and large cells, the latter predominating. Fibers enter it as axons of the small cells of the caudate nucleus and putamen. The large cells of the *globus pallidus* give rise to efferent fibers.

The *globus pallidus* has to do with automatic and associated movements and their control, and with muscular stabilization. Degeneration of this nucleus is responsible for the syndrome of juvenile paralysis agitans, characterized by increased muscle tone coupled with the attitude and body positions of Parkinson's disease.

The *caudate nucleus* is part of the neostriatum. A portion of its head, however, is connected with the base of the *stria terminalis* and is regarded as belonging to the paleostriatum. It is made up of multipolar cells which in the adult are pigmented. Many of the cells are of small to medium size, of Golgi's type II, with short axons. Some are large, with long axons and much Nissl substance.

Thalamostriatal fibers reach the caudate nucleus from the anterior and medial nuclei of the thalamus. There are also *internuclear fibers*. These take origin in small cells of the caudate nucleus and the putamen, terminating chiefly in the medial and lateral parts of the *globus pallidus*. The caudate nucleus is regarded as normally exerting inhibitory influences on the *globus pallidus*.

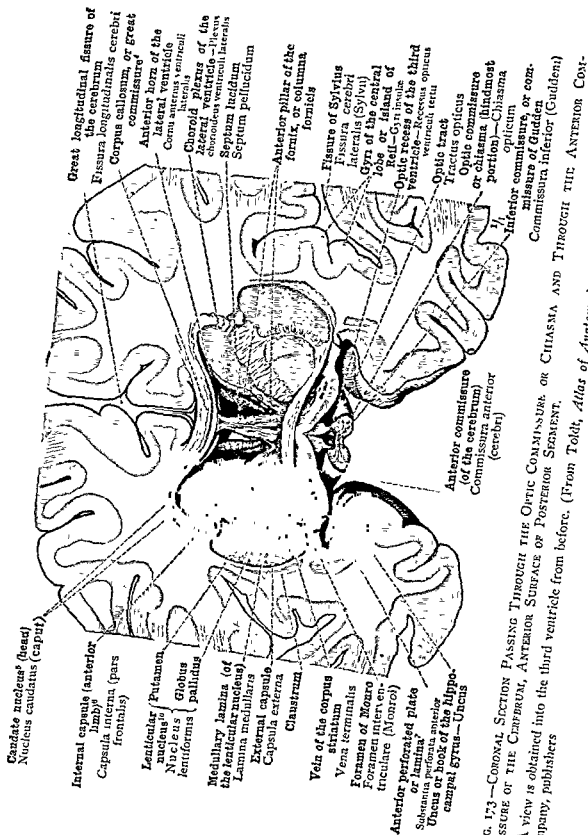


FIG. 173.—CORONAL SECTION PASSING THROUGH THE OPTIC COMMISSURE OR CHIASSMA AND THROUGH THE ANTERIOR COMMISSURE OF THE CEREBRUM, ANTERIOR SURFACE OF POSTERIOR SEGMENT.
A view is obtained into the third ventricle from before. (From Todd, *Atlas of Anatomy*.) By permission of The Macmillan Company, publishers

Morgan regards the motor disturbances associated with degeneration in the striate body as due to irritative stimulation of these nuclei rather than loss of function by them.

The *putamen* is the larger part of the lentiform nucleus. As already stated, it is continuous with the caudate nucleus in front of the internal capsule, the two together forming the *neostriatum*. There are large and small cells, the latter being more numerous. The large cells resemble those of large size in the globus pallidus.

Efferent fibers from the striate body, having their origin chiefly in the large cells of the globus pallidus, reach (1) the thalamus; (2) the substantia nigra; (3) the red nucleus; (4) the subthalamus; (5) the nucleus of the medial longitudinal bundle (nucleus of Darkschewitsch) of the opposite side, and probably the motor Vth and motor VIIth nuclei. They constitute the *ansa lenticularis*, a large bundle of fibers running transversely, in large part. Fibers derived from the ansa pass caudally through field H of Forel as the lenticular fasciculus which terminates in the red nucleus.

THE WHITE MATTER

The deep part of the cerebral hemispheres consists of numerous bundles of myelinated fibers and neuroglia. The fibers constitute three systems, distinct in their course and connections, namely, projection fibers, commissural fibers and association fibers.

The *projection fibers* include all of the afferent and efferent bundles which connect the cortex with the brain stem and spinal cord. They pass through the brain stem and the internal capsule. On emerging from the latter they spread out toward the different parts of the cortex, forming the *corona radiata*.

The *commissural fibers* connect the two cerebral hemispheres. They are grouped into three masses, namely, the corpus callosum, the hippocampal commissure, and the anterior commissure. The posterior and habenular commissures connect nuclear masses in the brain stem and therefore belong in a somewhat different category.

The *corpus callosum* (Fig. 173) is the largest of the commissures, forming a band between the two hemispheres which is attached to them through nearly half of their long axis. It is divided into a posterior, thickened and rounded end called the *splenium*; an anterior, less massive part, the *genu*; and the main body of the corpus callosum, or *trunk*, which lies between. The genu is turned downward and backwards, tapering as it curves caudally. The tapering part is known as the *rostrum*.

Within the hemispheres the fibers spread out in such a manner that they reach most of the cerebral cortex, intersecting the fibers of the corona radiata. The mass constitutes the radiations of the corpus callosum. The occipital part of this radiation, from the splenium, curves sharply backward into the occipital

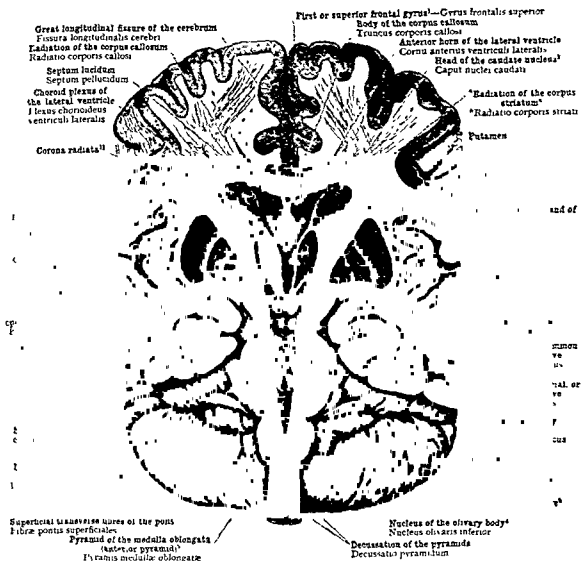


FIG. 174.—TRANSVERSE SECTION THROUGH THE BRAIN IN THE DIRECTION OF THE MEDULLA OBLONGATA AND THE CEREBRAL PEDUNCLES OR CRURA CEREBRI; THE COURSE OF THE PYRAMIDAL TRACT FROM THE DECUSSATION OF THE PYRAMIDS UPWARDS THROUGH THE PYRAMIDS OF THE MEDULLA OBLONGATA (ANTERIOR CRUS CEREBRI) INTO THE INTERNAL CAPSULE, WHERE IT ENTERS THE PEDUNCLE OF THE CORONA RADIATA (PEDUNCULUS CORONAE RADIATAE).

In the medullary center or white matter of the cerebrum (Medullum) we see the interlacement of the radiation of the corpus callosum (radiation corporis callosi) with the fibers of the corona radiata as they diverge from the internal capsule, and with the fibers of the radiation of the corpus striatum (radiation corporis striati). (From Toldt, *Atlas of Anatomy*) By permission of The Macmillan Company, publishers.

Morgan regards the motor disturbances associated with degeneration in the striate body as due to irritative stimulation of these nuclei rather than loss of function by them.

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THE CEREBRAL HEMISPHERES

The *habenular commissure* connects the habenular bodies which lie in front of the pineal body. It is related to the olfactory system.

THE ASSOCIATION FIBERS

In contrast with the commissural fibers, which connect corresponding parts of the two hemispheres, the association fibers (Fig. 175) unite different parts of the same hemisphere. They are regarded as made up of fibers running in

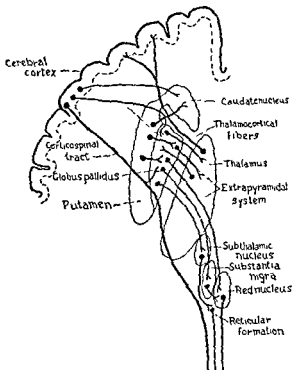


FIG 176—DIAGRAM OF SOME CONNECTIONS OF BASAL NUCLEI

both directions. Some connect adjacent gyri and are known as *short association fibers*. Others connect distant parts of the hemisphere, forming the *long association fibers*. They distribute and diffuse the impulses brought to the cortex by the ascending projection systems. Through the association bundles the different regions of the cortex are enabled to function in coördination with each other.

The *short association bundles* or *fibræ propriae* arise from cells in the gyri and arch beneath the floor of the intervening sulci, to end in the cortex of adjacent gyri. Bundles of the long association fibers form distinct bands which can be exposed by dissection and have been given specific names, as follows:

The *cingulum* or *girdle* is a band of white fibers within the gyrus cinguli. It connects the anterior perforated substance with the dentate gyrus, taking "course over the corpus callosum.

lobe. A band of fibers from the splenium curves over and around the posterior horn of the lateral ventricle as the *tapetum*.

The *hippocampal commissure* is a thin sheet of transverse fibers which lies close to the under side of the posterior portion of the body of the corpus callosum. It connects the medial margins of the limbs of the fornix and therefore has a triangular form. Its fibers are axons of pyramidal cells of the hippocampus which make up part of the alveus and the fimbria before reaching the crus of the fornix. They terminate in the molecular layer of the opposite hippo-

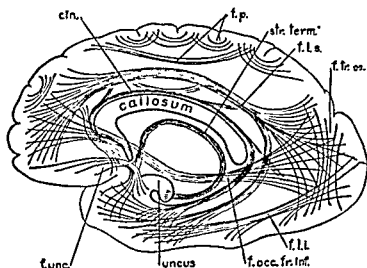


FIG. 175.—DIAGRAM OF ASSOCIATION BUNDLES IN CEREBRAL HEMISPHERE.

cin., cingulum; *f.l.i.*, inferior longitudinal fasciculus; *f.l.s.*, superior longitudinal fasciculus; *f.off.fr.inf.*, inferior occipitofrontal fasciculus; *f.p.*, arcuate fibers; *f.fr.oc.*, transverse occipital fasciculus; *f.unc.*, uncinate fasciculus; *str. term.*, stria terminalis. From Herrick, *Introduction to Neurology*, W B Saunders Co, Philadelphia, 1931.

campus. The hippocampal commissure connects the cortex of the rhinencephalon, one side with the other.

The *anterior commissure* (Fig. 173) crosses the median plane in the anterior wall of the third ventricle in the zone between the rostrum of the corpus callosum and the lamina terminalis. The fibers are of two groups: (1) fibers of the rhinencephalon connecting the olfactory areas, pyriform areas and amygdaloid nuclei of the two sides; (2) neopallial fibers which fray out in the temporal lobes.

The *posterior commissure* belongs chiefly to the midbrain but appears to contain some fibers connecting diencephalic structures. It crosses the midplane below the stalk of the pineal body in the anterior end of the midbrain roof. Its fibers are derived from several sources, but are not clearly understood. Some appear to arise in the superior colliculus, others in the nucleus of Darkschewitsch, and some are regarded as decussating fibers of the medial longitudinal bundle, which is believed by some authors to have its origin from the nucleus of Darkschewitsch

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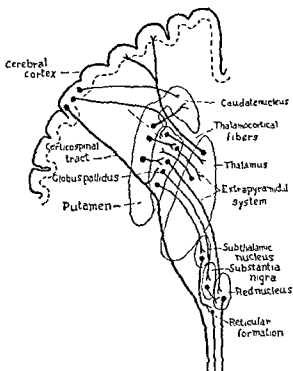


FIG 176—DIAGRAM OF SOME CONNECTIONS OF BASAL NUCLEI

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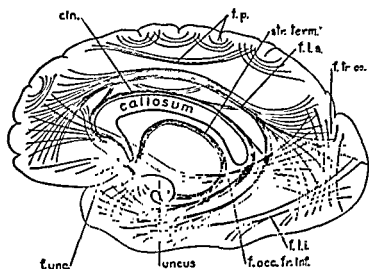


FIG. 175—DIAGRAM OF ASSOCIATION BUNDLES IN CEREBRAL HEMISPHERE.

cin., cingulum; *f.li.*, inferior longitudinal fasciculus; *f.l.s.*, superior longitudinal fasciculus; *f.offr.inf.*, inferior occipitofrontal fasciculus; *f.p.*, arcuate fibers; *f.tr.oc.*, transverse occipital fasciculus; *func.*, uncinat fasciculus; *str.term.*, stria terminalis. From Herrick, *Introduction to Neurology*, W B Saunders Co., Philadelphia, 1931.

campus. The hippocampal commissure connects the cortex of the rhinencephalon, one side with the other.

The *anterior commissure* (Fig. 173) crosses the median plane in the anterior wall of the third ventricle in the zone between the rostrum of the corpus callosum and the lamina terminalis. The fibers are of two groups: (1) fibers of the rhinencephalon connecting the olfactory areas, pyriform areas and amygdaloid nuclei of the two sides; (2) neopallial fibers which fray out in the temporal lobes.

The *posterior commissure* belongs chiefly to the midbrain but appears to contain some fibers connecting diencephalic structures. It crosses the midplane below the stalk of the pineal body in the anterior end of the midbrain roof. Its fibers are derived from several sources, but are not clearly understood. Some appear to arise in the superior colliculus, others in the nucleus of Darkschewitsch, and some are regarded as decussating fibers of the medial longitudinal bundle, which is believed by some authors to have its origin from the nucleus of Darkschewitsch.

THE CEREBRAL HEMISPHERES

The *medial* and *lateral longitudinal striae*, in part, connect the subcallosal gyrus and anterior perforated space with the hippocampal formation.

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A TEXTBOOK OF NEURO-ANATOMY AND THE SENSE ORGANS

The *superior longitudinal bundle* connects the frontal lobe with the occipital and temporal lobes. Its fibers, in part, arch over the lentiform nucleus and the island of Reil and downward behind the corpus callosum. The uppermost fibers of the bundle take a more direct course.

The *inferior longitudinal bundle* takes its course along the lateral walls of the inferior and posterior horns of the lateral ventricle, connecting the temporal and occipital lobes.

The *occipitofrontal bundle* takes its course along the lateral margin of the

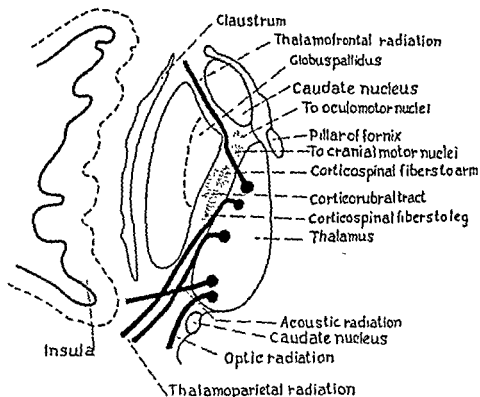


FIG. 177.—DIAGRAM OF INTERNAL CAPSULE AND SOME CONNECTIONS OF THE THALAMUS.

caudate nucleus and the middle part of the corona radiata. The fibers spread out like a fan lateral to the posterior and inferior horns of the ventricle, connecting the occipital and frontal lobes.

The *uncinate bundle* arches beneath the fissure of Sylvius and connects the frontal lobe with the forward end of the temporal lobe.

The *transverse occipital bundle* connects the tentorial part of the occipital lobe with the upper medial and lateral parts of this lobe and with neighboring parts of the parietal lobe.

The *stria terminalis of the thalamus* connects the anterior perforated substance with the amygdaloid nucleus, and may be regarded as an association bundle.

VENTRICLES OF THE BRAIN AND CHORIOID PLEXUS

the stria terminalis, the lamina affixa, covering the thalamus, and the chorioid plexus. Medially it is bounded by the edge of the body of the fornix and part of the septum pellucidum.

The *inferior horn* curves around the thalamus, in a caudolateral direction, into the temporal lobe. Within this it curves downward, forward and somewhat inward. The roof is the tapetum, the floor is chiefly the hippocampus.

The *posterior horn* curves backward from the body of the ventricle into the

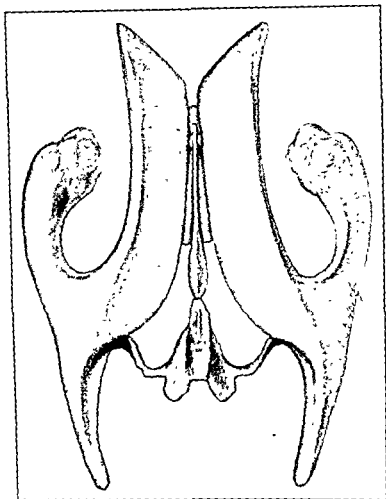


FIG 178.—DORSAL VIEW OF CAST OF VENTRICLES. (After Retzius.)

occipital lobe. Its walls are lateral and medial, the former being concave and the latter convex. The superior part of the lateral wall is formed by the tapetum. The greater part of the boundaries of this portion of the lateral ventricle is formed by the white substance of the occipital lobe. A ridge on the inner wall represents the *calcar avis*, formed in the floor of the deeply penetrating calcarine fissure.

The **THIRD VENTRICLE** has been partly described in connection with the diencephalon. It is an unpaired, cleft-like cavity lined with ependyma. Rostrally

CHAPTER 19

VENTRICLES OF THE BRAIN AND CHORIOID PLEXUS

VENTRICLES

The ventricles are the cavities formed by folding of the rostral part of the neural plate. They are continuous with the central canal of the spinal cord, but constitute large, irregular spaces, normally filled with cerebrospinal fluid. There are four ventricles, named respectively, the *lateral* (first and second) in each cerebral hemisphere; the *third*, in the diencephalon, extending slightly into the telencephalon; and the *fourth*, the cavity of the medulla oblongata.

The *interventricular foramen* (*foramen of Monro*) on each side connects the lateral ventricle with the third ventricle. This is a small, rounded opening 2 to 4 mm. in diameter through which the lateral ventricles communicate with each other, indirectly, as well as directly with the third ventricle. Due to the great extension of the hemispheres backward in the development of the brain, the foramen of Monro opens into the rostral part of the adult lateral ventricle. The *cerebral aqueduct* (*aqueduct of Sylvius*) connects the third and fourth ventricles. This is a narrow passageway about 15 mm. long, lying between the quadrigeminal plate and the tegmentum of the midbrain. The central part is somewhat expanded and was called the *ventricle of the midbrain* by Retzius. It is surrounded by the central gray substance of the midbrain.

The **LATERAL VENTRICLE** on each side is an elongated curved cavity divided into *anterior horn* or *cornu*, *body* or *pars centralis*, *posterior horn* and *inferior horn* (Figs. 178 and 179).

The *anterior horn* or *cornu* extends from the foramen of Monro into the frontal lobe. In the embryo it continues into the olfactory bulb, but this cavity becomes obliterated in the human adult. It is bounded above, partly below, and rostrally by radiating fibers of the corpus callosum. The lateral wall and part of the floor is formed by the head of the caudate nucleus, the ventricle curving laterally in front of the latter. The medial wall is formed by the septum pellucidum. Chorioid plexus extends through the foramen of Monro into the anterior horn, forming part of its floor.

The *body* (*pars centralis*) is a horizontal cleft extending from the foramen of Monro to the region of the splenium of the corpus callosum, where it divides into anterior and posterior parts. The lateral part of the cleft inclines forward toward the anterior horn. The roof of the body is formed by the corpus callosum. The lateral floor is formed chiefly by the caudate nucleus. More medially lies

VENTRICLES OF THE BRAIN AND CHORIOID PLEXUS

the stria terminalis, the lamina affixa, covering the thalamus, and the chorioid plexus. Medially it is bounded by the edge of the body of the fornix and part of the septum pellucidum.

The *inferior horn* curves around the thalamus, in a caudolateral direction, into the temporal lobe. Within this it curves downward, forward and somewhat inward. The roof is the tapetum, the floor is chiefly the hippocampus.

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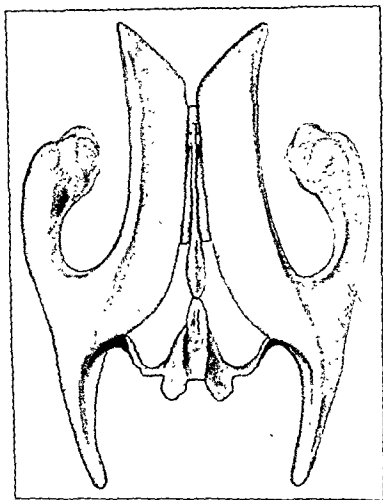


FIG. 178.—DORSAL VIEW OF CAST OF VENTRICLES. (After Retzius.)

occipital lobe. Its walls are lateral and medial, the former being concave and the latter convex. The superior part of the lateral wall is formed by the tapetum. The greater part of the boundaries of this portion of the lateral ventricle is formed by the white substance of the occipital lobe. A ridge on the inner wall represents the *calcar avis*, formed in the floor of the deeply penetrating calcarine fissure.

The **THIRD VENTRICLE** has been partly described in connection with the diencephalon. It is an unpaired, cleft-like cavity lined with ependyma. Rostrally

it is bounded by the lamina terminalis, the anterior commissure and the pillars of the fornix. Posterior boundaries are the habenular and posterior commissures, below which it continues into the aqueduct of Sylvius. The lateral walls are formed by the medial surfaces of the thalamus and the hypothalamus. The roof is formed by a thin epithelial layer, attached to the upper surface of the habenulae and more rostrally, to the tænia of the thalamus. Above the epithelial plate lies the chorioid plexus of the third ventricle.

The *FOURTH VENTRICLE* tapers rostrally and caudally and has a wide *lateral recess* on each side. The narrow rostral part continues into the aqueduct of Sylvius. The caudal part tapers like a penpoint, and is called the *calamus scriptorius*.

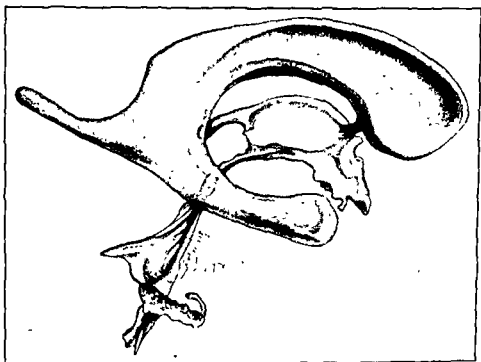


FIG 179—LATERAL VIEW OF CAST OF VENTRICLES. (After Retzius.)

torius. It continues into the central canal of the cord. The floor of this ventricle, known as the *rhomboid fossa*, is formed of various areas and nuclear eminences of the medulla oblongata. The upper part of the roof is formed by the anterior medullary velum and the cerebellum. The immediate roof of the caudal part of the ventricle is a layer of epithelium as in the third ventricle, above which lies the chorioid plexus. At the tip of each lateral ventricle there is an opening in the chorioidal roof known as the *foramen of Key-Retzius* or *foramen of Luschka*. A similar opening, the *foramen of Magendie*, occurs above the calamus scriptorius. This is considered by many to be an artefact. Through these openings the ventricular system has its communication with the subarachnoid space.

THE CHORIOID PLEXUS AND CEREBROSPINAL FLUID

The *chorioid plexus* (Fig. 180) is a rich network of pial blood vessels in the lateral ventricles and in the third and fourth ventricles of the brain. Folds of pia mater, known as the *tela choriodea*, with tufts of blood vessels, push into

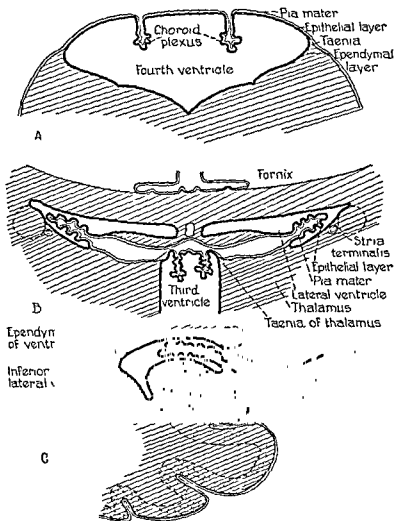


FIG. 180.—DIAGRAM OF CHOROID PLEXUSES.

the brain cavities through the thin, ependymal roofs of the third and fourth ventricles and through the similar chorioid fissures of the lateral ventricles. Carrying the ependyma before them, they form a tortuous mass with villus-like projections. The chorioid plexuses of the lateral and of the third ventricles are continuous at the foramina of Monro. In the lateral ventricle the plexus lies chiefly in the body, following the curve of the caudate nucleus and fimbria of the fornix to the tip of the inferior horn in the temporal lobe. The anterior and posterior horns of the lateral ventricle are devoid of chorioid plexus.

The *chorioid tela* of the third ventricle (*velum interpositum*) forms a duplication of pia mater between the fornix, on the one hand, and the thalamus and

it is bounded by the lamina terminalis, the anterior commissure and the pillars of the fornix. Posterior boundaries are the habenular and posterior commissures, below which it continues into the aqueduct of Sylvius. The lateral walls are formed by the medial surfaces of the thalamus and the hypothalamus. The roof is formed by a thin epithelial layer, attached to the upper surface of the habenulae and more rostrally, to the taenia of the thalamus. Above the epithelial plate lies the chorioid plexus of the third ventricle.

The FOURTH VENTRICLE tapers rostrally and caudally and has a wide *lateral recess* on each side. The narrow rostral part continues into the aqueduct of Sylvius. The caudal part tapers like a penpoint, and is called the *calamus scriptorius*.

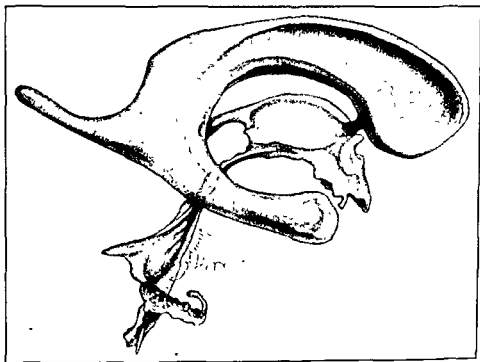


FIG. 179.—LATERAL VIEW OF CAST OF VENTRICLES. (After Retzius)

torius. It continues into the central canal of the cord. The floor of this ventricle, known as the *rhomboid fossa*, is formed of various areas and nuclear eminences of the medulla oblongata. The upper part of the roof is formed by the anterior medullary velum and the cerebellum. The immediate roof of the caudal part of the ventricle is a layer of epithelium as in the third ventricle, above which lies the chorioid plexus. At the tip of each lateral ventricle there is an opening in the chorioidal roof known as the *foramen of Key-Retzius* or *foramen of Luschka*. A similar opening, the *foramen of Magendie*, occurs above the calamus scriptorius. This is considered by many to be an artefact. Through these openings the ventricular system has its communication with the subarachnoid space.

VENTRICLES OF THE BRAIN AND CHORIOID PLEXUS

cerebrospinal fluid and dilatation of the cerebral ventricles. The direction of flow from the ventricles is downward through the foramina of Luschka into the space about the *medulla oblongata*. Some cerebrospinal fluid may be regarded as formed in the subarachnoid space by the chorioid plexus projecting through the foramina of Luschka. From the perimedullary space the fluid reaches other parts of the subarachnoid system.

By replacing the cerebrospinal fluid with air through injection directly into the ventricles the outlines of the latter can be determined with the x-ray. Changes in shape, due to growths or pressure, can be detected. A knowledge of the boundaries of the ventricles is important in interpreting such photographs.

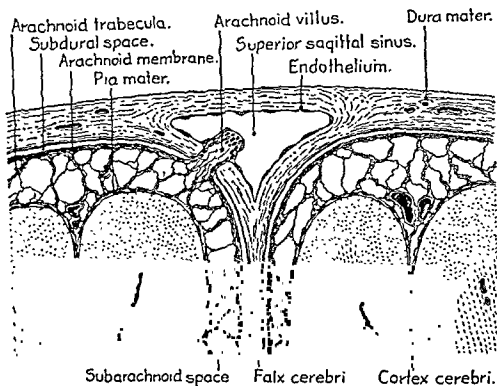


FIG. 181.—CORONAL SECTION OF MENINGES AND CEREBRAL CORTEX TO SHOW RELATION OF ARACHNOID VILLI TO DURAL VENOUS SINUS. (From L. H. Weed)

The *subarachnoid space* (Figs. 181 and 182) of the cranial cavity, like that of the spinal canal, lies between the pia mater and the arachnoid coat. In the cranium the latter is a thin, avascular membrane, separated from the dura mater by a thin subdural space which contains a small amount of *subdural fluid*. The arachnoid coat entirely covers the brain, and continues over the cord. It does not, however, dip into the sulci or fissures, and at the base of the brain there are large subarachnoid cavities or *cisterns*. The result is that over the gyri there is but a thin layer of cerebrospinal fluid. In the fissures and sulci the layer is deeper, according to the depth of the furrows.

The *cerebellomedullary cistern* (*cisterna magna*) is the largest of the sub-

third ventricle, on the other hand. From the floor of the space the chorioid plexus hangs into the ventricle on each side of the midline as a lobulated, longitudinal mass, separated from the ventricular cavity by ependyma.

A longitudinal strand of blood vessels invaginates the ependymal roof of the fourth ventricle on each side of the midline. At the base of the triangle formed by the tela of the ventricle the two plexuses join. From each side an extension passes into the lateral recess and projects into the subarachnoid space through the foramen of Luschka. The chorioid plexus of the fourth ventricle is more extensive than that of the third ventricle.

The CEREBROSPINAL FLUID is formed in the chorioid plexus, as shown by experimental methods. It has been suggested that slight additions come from the perivascular spaces in the brain, cord and meninges. Possibly ependymal cells of the ventricles and spinal canal add to it. There are indications of secretory cells in certain areas of the ventricular ependyma. The rate of formation varies with a number of factors, among which are hydrostatic pressure of the blood, variations in venous pressure, changes in osmotic pressure of the blood, etc.

As to method of formation, two theories have been advanced, namely, (1) that the cerebrospinal fluid is secreted by the epithelial cells of the plexus, (2) that the plexus acts as a dialysing membrane through which the cerebrospinal fluid forms in equilibrium with blood pressure. Both views have experimental and clinical support, but neither one has been demonstrated to the exclusion of the other.

[The cerebrospinal fluid functions as a mechanical protection of the brain and cord. It helps support the weight of the brain, serves as a buffer, etc. It has also been suggested that the fluid carries away from the central nervous system certain products of metabolic activity of nerve cells. Cushing holds that it receives and distributes part of the secretion of the posterior lobe of the hypophysis.]

The ependymal epithelium lining the chorioid plexuses is greatly increased in area by the numerous tufts of vessels pushing into it. A total area of more than one square meter has been estimated in man. The cells are cuboidal epithelium of ectodermal origin, arranged in a single layer. They may contain inclusions or fatty droplets. The free surface has been described as showing a brush border. Cilia also have been described. The epithelial cells are regarded as secretory and possibly selectively absorptive. Clark (1928) has demonstrated nerve fibers in the chorioid plexuses by histological methods. Finesinger and Putman (1933) have shown that constriction of the vessels of the chorioid plexus is produced by stimulation of the cervical sympathetic trunk, while dilatation results from stimulating the vagus.

The cerebrospinal fluid collects in the ventricles. The total amount appears to vary greatly, 65 to 180 c.c. being reported. Undue secretion of fluid or obstructions in the normal channels of the ventricular system, such as in the foramen of Monro, the aqueduct of Sylvius or the apertures of the fourth ventricle, may cause hydrocephalus, in which there is an increased amount of

perivascular space is regarded as a continuation of the subarachnoid space. Whether or not it extends to the smaller divisions of the blood vessels is disputed.

Arachnoid villi (pacchionian bodies) are elevations of the arachnoid which project into the superior sagittal sinus, especially. They are attached to the arachnoid by a stalk, through which the subarachnoid space continues into the cavity of the villus. The arachnoid villi provide the chief outlet for cerebrospinal fluid into the venous circulation. Dyes injected into the subarachnoid space have been recovered in the blood stream in ten to thirty seconds. They have not been found in the lymphatics until much later.

A knowledge of the subarachnoid cisterns and the channels leading from them is of importance in encephalography. By displacing the cerebrospinal fluid of the subarachnoid space with air, as in ventriculography, x-ray pictures can be made of the outlines of the brain surface and of abnormalities in the width of the subarachnoid space.

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arachnoid spaces in the cranial cavity. It is produced by the bridging of the arachnoid from the posterior part of the inferior cerebellar surface to the dorsal surface of the medulla oblongata. The fluid in this cavity is continuous with that of the subarachnoid space of the spinal cord. Through the apertures leading from the fourth ventricle it is also continuous with the fluid of this ventricle.

The *pontine cistern* (*cisterna pontis*) is continuous with the cisterna magna and with the subarachnoid space surrounding the medulla oblongata.

The *interpeduncular cistern* (*cisterna interpeduncularis*) lies in front of the pons, in the deep hollow formed between the cerebral peduncles. A considerable



FIG. 182.—DIAGRAM OF SUBARACHNOID SPACE, SHOWING RELATION TO NERVOUS TISSUE.
(From L. H. Weed.)

channel leads toward the fissure of Sylvius on each side. It contains the middle meningeal artery.

The *chiasmatic cistern* (*cisterna chiasmatis*) lies in front of the optic chiasma. Between the hemispheres the cistern of the chiasma continues upward in front of the corpus callosum. The anterior meningeal artery lies in this space.

The blood vessels to and from the brain pass through the subarachnoid space. They become surrounded as they penetrate into the nervous tissue by two layers of connective tissue between which is a space (Virchow-Robin), bridged at intervals by connective tissue strands. The inner wall of this space is a continuation of the arachnoid, merged with the tunica adventitia of the blood vessel. The outer sheath is formed of a layer of pia mater, astrocytes, etc. The

THE OPTIC SYSTEM

the greater part of the cup is found the nervous zone or *pars optica*. The boundary of the two in the adult is formed by a wavy line encircling the retina, known as the *ora serrata*.

The lens develops from the outside ectoderm. A thickening of epithelium, the anlage of the lens, is first formed opposite the optic cup (Fig. 185). This invaginates into a vesicle and eventually is pinched off from the external ectoderm in such a manner that it lies at the opening of the optic cup, nearly filling

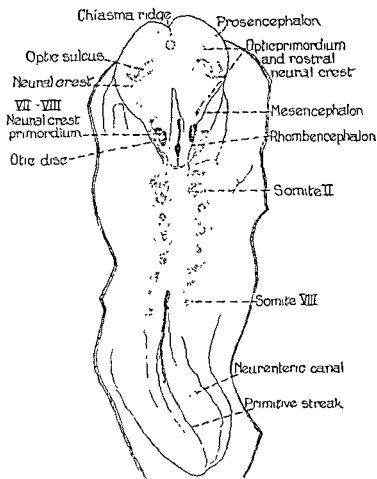


FIG 183—EARLY DEVELOPMENT OF HUMAN RETINA.

Redrawn from Bartelmev and Evans

the cavity of the latter. In embryos of 8 mm., it has become a sac with a thin wall toward the body surface and a thick wall on the side toward the retina. The thin portion of the wall is formed of low columnar epithelium and becomes the *lens epithelium*. The thick inner wall is formed of tall cells which continue to increase in length so that in embryos of about seven weeks the lens cavity has been obliterated. The elongated cells lose their nuclei and the cells become the *lens fibers*. After the beginning of the third month of development additional lens fibers are formed from cells of the epithelial layer. A *capsule* is formed about the lens from the epithelium.

CHAPTER 20

THE OPTIC SYSTEM

The optic or visual system consists of the eye, optic nerves, optic chiasma, optic tracts and the nuclei in which the latter terminate. These nuclei are made up of cell masses in the superior colliculus, the tegmentum of betweenbrain and midbrain, and the lateral geniculate body. The superior colliculus and tegmentum are centers for reflex optic connections. From the lateral geniculate body fibers pass to the cortex of the occipital lobe as the optic radiations. These end chiefly in the region of the cuneus, which serves conscious vision.

THE EYE

The eye is a complex organ whose neuro-epithelial sensory part, the retina, is so dependent upon accessory structures for its proper functioning that the entire organ will be described. The retina itself is derived from the forebrain. Bartelmez has shown that the optic *placode*, the thickening of the brain wall which gives rise to the retina, is present in a human embryo of 4 mm., in the open neural plate stage. As the neural plate folds up the thickened part which forms the optic placode assumes a lateral position on each side (Figs. 183 and 184). The placode pushes outward, forming an *optic vesicle* by the 4 mm. stage. By invagination of the outer part of the wall of the vesicle, an *optic cup* is formed which remains attached to the forebrain wall by a hollow *optic stalk* (Fig. 185). The invagination extends along the ventral side of the optic stalk toward the brain, forming a fissure in the lower part of the optic cup. This is the *chorioid fissure*. Normally it closes during the sixth or seventh week of embryonic life, so that the optic cup becomes complete, with a circular rim. In the meantime, however, a blood vessel has entered the optic stalk and optic cup through this fissure. As the margins of cup and fissure meet, the blood vessel becomes enclosed. It becomes the central artery of the retina.

The invagination of the optic vesicle results in two layers of the optic cup. The inner layer develops into many strata of cells and becomes the retina proper. The outer layer acquires a pigment, *fuscin*, and becomes the thin *pigmented layer*. The space between the two layers disappears with the growth of the retina so that the pigmented cells of the outer layer come to lie against the outer, or rod and cone, layer of cells of the invaginated portion.

Two regions may be recognized in the inner or retinal layer of the optic cup. Bordering its margin there is a non-nervous zone, the *pars caeca*, and occupying

THE OPTIC SYSTEM

surface of the lens. This is the *anterior chamber*. The stroma of the iris, formed from the mesoderm of the chorioid layer, together with a layer of pigmented epithelium from the pigment layer of the retina and the pars caeca of the retina, anterior to the ora serrata, form the curtain-like *iris*. This separates the anterior chamber from the lens save at the *pupil*. It also separates the anterior chamber from the *posterior chamber*, which lies between the iris and the suspensory ligaments of the lens.

The nervous layer of the retina increases in thickness by proliferation of cells. The outermost layer of cells becomes differentiated into the neuro-epithelial *rod* and *cone cells*. The nuclei of these cells form many layers but this indicates merely a pseudostratification. Another zone of many layers of



FIG 185—DIAGRAM REPRESENTING STAGES OF INVAGINATION OF OPTIC AND LENS VESICLES.

A, cavity of the optic vesicle; *B*, cavity of the optic cup, *C*, lens vesicle. From Cowdry, *Special Cytology*, Paul B. Hoeber, Inc., New York, 1932.

nuclei is due to the *bipolar cells* which are nerve cells. The innermost layer of cells is made of the large *ganglion cells*. These cells give rise to nerve fibers which converge from all parts of the nervous region of the retina toward the chorioid fissure while that is still open. They enter the fissure and extend, by growth in length, along the optic stalk toward the brain. On reaching the brain they decussate as the optic chiasma, and continue their growth to the optic centers. These fibers constitute the optic nerve and optic tract. As the chorioid fissure of the retina closes up the fibers become encased by the retinal walls as a bundle which passes through the retina. This is the *head* of the optic nerve. The optic stalk is gradually attenuated by the drawing of the eyeball farther and farther away from the brain, as the head develops. Eventually its connection with the brain is lost or it remains as a fibrous strand along the optic nerve which used the stalk as a bridge to the brain in its own development.

A condensation of mesenchyma forms a *dural sheath* around the optic nerve which corresponds to the dura mater of the brain. A thinner immediate covering constitutes the *pial sheath*. The sclera of the eyeball is regarded embryologically as corresponding to the dura mater, and the chorioid to the pia of the brain.

In the adult the cornea forms the anterior segment of a sphere with a radius of about 8 mm, attached to a larger posterior segment, the sclera, whose radius is about 12 mm. The line of attachment is called the sulcus of the sclera. The

The lens can be formed from ectoderm of other parts of the body than that normally found over the optic cup. Lewis transplanted flank ectoderm to the optic cup region, in frog tadpoles, and obtained well formed lenses. Apparently there is some interaction between the developing optic cup and the skin ectoderm which results in the modification of the latter.

While these developmental processes are taking place in the ectodermal derivatives, mesoderm has formed about the optic cup. Mesenchymal cells have migrated between the lens and the outside ectoderm, and also into the cavity of

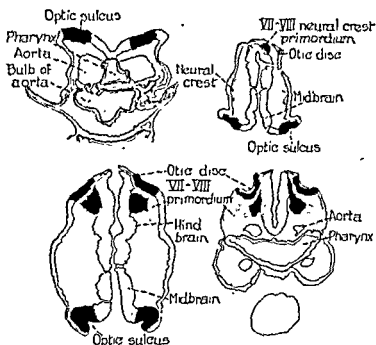


FIG. 184—SECTIONS SHOWING EARLY STAGES IN FORMATION OF HUMAN OPTIC CUP.

Redrawn from Bartelmev and Evans.

the optic cup. The mesenchymal cells within the cup remain in an embryonic condition. They give rise to the vitreous body which fills the cavity of the eyeball behind the lens.

The mesenchyme in front of the lens and in contact with the pigment layer of the retina condenses into a firm layer. In front of the lens this becomes the fibrous part of the cornea, an *anterior* and a *posterior* layer of epithelium being added. The mesoderm external to the pigment layer becomes the scleral and the chorioid coats of the eyeball. The former is the outer coat and is continuous with the cornea. The *chorioid coat* acquires numerous blood vessels by the sixth week of the embryo, these vessels being the chief supply of the eye. Beyond the ora serrata the chorioid layer differentiates into the unstriated *ciliary muscle*, the folds of the *ciliary bodies*, and the *stroma of the iris*.

A space develops in the mesenchyme between the cornea and the anterior

surface of the lens. This is the *anterior chamber*. The stroma of the iris, formed from the mesoderm of the chorioid layer, together with a layer of pigmented epithelium from the pigment layer of the retina and the pars caeca of the retina, anterior to the ora serrata, form the curtain-like *iris*. This separates the anterior chamber from the lens save at the *pupil*. It also separates the anterior chamber from the *posterior chamber*, which lies between the iris and the suspensory ligaments of the lens.

The nervous layer of the retina increases in thickness by proliferation of cells. The outermost layer of cells becomes differentiated into the neuro-epithelial *rod* and *cone cells*. The nuclei of these cells form many layers but this indicates merely a pseudostratification. Another zone of many layers of



FIG. 185—DIAGRAM REPRESENTING STAGES OF INVAGINATION OF OPTIC AND LENS VESICLES.

A, cavity of the optic vesicle, B, cavity of the optic cup, C, lens vesicle. From Cowdry, *Special Cytology*, Paul B Hoeber, Inc, New York, 1932.

nuclei is due to the *bipolar cells* which are nerve cells. The innermost layer of cells is made of the large *ganglion cells*. These cells give rise to nerve fibers which converge from all parts of the nervous region of the retina toward the chorioid fissure while that is still open. They enter the fissure and extend, by growth in length, along the optic stalk toward the brain. On reaching the brain they decussate as the optic chiasma, and continue their growth to the optic centers. These fibers constitute the optic nerve and optic tract. As the chorioid fissure of the retina closes up the fibers become encased by the retinal walls as a bundle which passes through the retina. This is the *head* of the optic nerve. The optic stalk is gradually attenuated by the drawing of the eyeball farther and farther away from the brain, as the head develops. Eventually its connection with the brain is lost or it remains as a fibrous strand along the optic nerve which used the stalk as a bridge to the brain in its own development.

A condensation of mesenchyma forms a *dural sheath* around the optic nerve which corresponds to the dura mater of the brain. A thinner immediate covering constitutes the *pial sheath*. The sclera of the eyeball is regarded embryologically as corresponding to the dura mater, and the chorioid to the pia of the brain.

In the adult the cornea forms the anterior segment of a sphere with a radius of about 8 mm., attached to a larger posterior segment, the sclera, whose radius is about 12 mm. The line of attachment is called the sulcus of the sclera. The

axis between the central points of the two segments is known as the *axis of the eye* (*axis oculi*).

BULBAR FASCIA.—The eyeball is surrounded by a thin fibrous capsule, the *fascia of the bulb* or *capsule of Tenon*, which extends from the entrance of the optic nerve to the junction of sclera and cornea. Between the fascia and the sclera lies the *episcleral space* which serves as a cavity, containing a small amount of fluid in which the eyeball rotates. The space is crossed by many fine strands of connective tissue. The fascia bulbi is penetrated by the tendons of the external eye-muscles which attach to the sclera. The fascia is reflected along these tendons and becomes continuous with the thin muscle sheaths of the individual muscles. Slips from the muscle sheaths attach to the wall of the orbit and are regarded as serving to check the pull of their respective muscles, hence they are called *check ligaments*. A band of connective tissue, the *suspensory ligament* of Lockwood, passes like a hammock beneath the eyeball. Its ends are attached through the check ligaments of the medial and lateral rectus muscles to the respective orbital walls. This ligament is formed by the junction of the margins of the muscle sheaths of the interior rectus with the margins of the lateral and medial rectus muscles.

SCLERA.—As indicated in the development of the eye, the sclera (Fig. 186) forms the outer layer of the bulb of the eye proper. It varies in thickness. Posteriorly it is 0.8 to 1 mm. thick, at the equator about 0.4 mm., and at the scleral sulcus about 0.6 mm. thick. It is a dense, tough layer composed of white fibrous connective tissue occurring in flattened bands which run parallel to the surface. The bands form both equatorial and meridional layers which interlace with each other. Some fine elastic fibers are intermingled, but they are relatively few. Connective tissue cells of various types are found in spaces between the fibers. In the innermost layer, the *lamina fusca*, numerous pigmented connective tissue cells occur. In children the sclera has a bluish tint because it is thinner than in the adult and, for this reason, the pigment of the chorioid coat shows through.

Posteriorly, about 3 mm. to the medial side of the posterior pole, there is a funnel-shaped opening in the sclera through which the optic nerve enters the eyeball by a series of perforations, the *lamina cribrosa* of the sclera (Fig. 192). The myelin sheaths of the optic fibers disappear at this point so that the inner part of the opening in the sclera, through which the naked nerve fibers pass, is narrower than the outer border. The sheath of the optic nerve is continuous with the outer part of the sclera. Small apertures, 15 to 20 in number, for the ciliary nerves and short ciliary arteries, and four openings, two above and two below, for the veins from the chorioid coat, penetrate the sclera near the entrance of the nerve. Anteriorly the sclera is penetrated near its sulcus by the anterior ciliary arteries. At the junction between sclera and cornea there is a circular canal, the *sinus venosus of the sclera*, or *canal of Schlemm*, which in section appears as a cleft. It is lined with endothelium and drains into the

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anterior ciliary veins, serving to carry off excess fluid from the anterior chamber of the eye

The external surface of the sclera, the *episclera*, is less dense and its bundles of fibers become more slender, with more numerous and coarser elastic fibers. There is a gradual transition into the loose tissue of Tenon's space. The episclera has a relatively rich blood supply, in contrast to the paucity of vessels in the sclera itself.

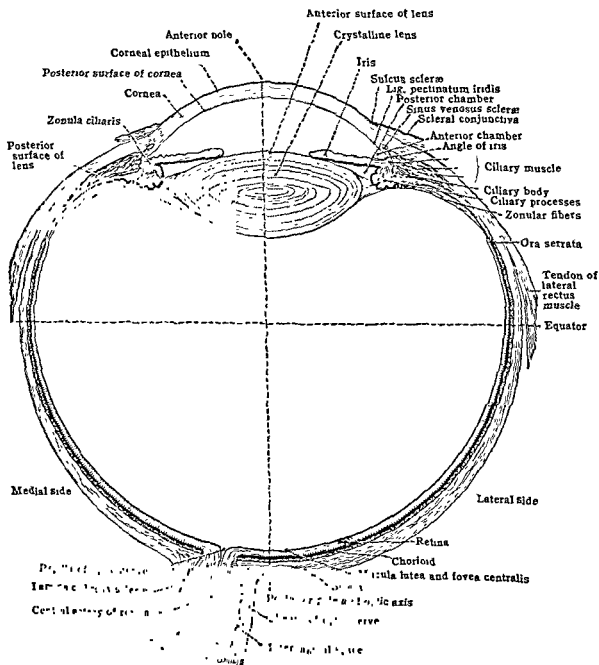


FIG 186—HORIZONTAL SECTION OF RIGHT EYEBALL.

From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co, Philadelphia, 1933

The CORNEA (Fig. 187) is continuous at the sclerocorneal junction with the tissue of the sclera. It consists, however, of five distinct layers with properties very different from those of the sclera. The outermost or epithelial layer, moreover, is derived from the outside ectoderm of the embryo, while the main mass of the cornea, like the sclera, is derived from mesoderm. Together with the lens of the eye and the vitreous body the cornea has the property of transparency, for which there has been offered no adequate histological explanation.

The layers of the cornea are as follows from without inward: (1) epithelium, (2) anterior elastic lamina or Bowman's membrane, (3) substantia propria, (4) posterior elastic lamina or Descemet's membrane, (5) endothelium of anterior chamber or Descemet's endothelium. The epithelial layer is five to six cells (37 to 58 microns) thick in man. Its surface is smooth. There are three zones, namely, (1) the superficial layer of flattened cells, three or four cells thick; (2) the intermediate layer, one cell thick; and (3) the basal layer, made of perpendicularly arranged columnar cells whose bases rest on Bowman's membrane.

Intercellular spaces are described between the basal cells, the narrower ones crossed by protoplasmic bridges. These spaces have not been traced beyond the intermediate layer of the epithelium, but they become wider toward Bowman's membrane. They contain a fluid called *epithelial lymph* by Flemming, which may harbor wandering leucocytes, pigment granules or fragmenting nuclei.

The *anterior elastic membrane*, also called *Bowman's membrane*, is 10 to 16 microns thick and merges into the substantia propria, of which it is the specialized surface layer. It differs from true elastic tissue in its staining qualities. At the margins of the cornea this membrane fades away into the substantia propria.

The *substantia propria* of the cornea appears homogeneous in the fresh condition, but when fixed it shows modified fibrous tissue with some elastic fibers. It makes up 90 per cent of the thickness of the cornea. The connective tissue is arranged in lamellae roughly parallel to the surface. Between these are spaces or lacunae of the cornea. These are irregularly stellate in form and communicate with each other. They contain flattened corneal cells and lymph. The corneal cells are greatly flattened, having a diameter of 12 to 27 microns and a thickness of but 2 microns. Their long, irregular processes form a network, described as made up of joined processes of adjacent cells. Migratory leucocytes are also found in these spaces.

The *posterior elastic layer*, or *Descemet's membrane*, is elastic in nature and tends to curl up when detached. Its staining reaction is also that of elastic tissue. It is a clear, acellular membrane, loosely attached to the substantia propria, and having a thickness of about 6 microns at the center and about 10 microns at the periphery of the cornea. It is a product of the endothelial cells which cover its deep surface and can be regenerated from these cells when injured.

The *endothelium of the anterior chamber*, or *Descemet's endothelium*, consists of a single layer of cells 18 to 20 microns in diameter and 5 microns thick.

These cells are regarded as highly specialized endothelial elements. The layer is reflected onto the anterior surface of the iris.

The Pectinate Ligament of the Iris.—At the junction of sclera and cornea Descemet's membrane splits into bundles of fine interlacing fibers, which form a triangular area known as the pectinate ligament of the iris. The spaces between the trabeculae of fibers, known as the *spaces of the angle of the iris* or *spaces of Fontana*, are lined with endothelium continuous with that of the anterior chamber, on the one hand, and with the endothelium of the venus sinus of the sclera or canal of Schlemm on the other hand. These spaces form the channels through which fluid from the anterior chamber may pass into the canal of Schlemm, which in turn drains into the anterior ciliary veins, as previously stated.

The *sinus venosus of the sclera* or *canal of Schlemm* appears in meridional section as a narrow cleft in the deeper part of the sclerocorneal junction. Its outer wall is formed by the sclera, but its inner wall is formed of the mass of trabeculae and spaces which constitute the pectinate ligament of the iris above described.

The CHORIOID COAT or CHORIOIDEA lies beneath the sclera, to which it is attached. It consists of loose connective tissue, blood vessels and pigmented connective tissue cells. In the fresh condition it is a soft, elastic membrane of brownish color, due to the pigment. Usually three layers are described, but Arey divides it into five layers, which, starting from the outside, are as follows (1) suprachoroid, (2) blood vessel layer, (3) supracapillary layer, (4) capillary layer, (5) elastic layer, which joins with the cuticular layer of the pigmented epithelium of the retina to form the *lamina basalis*. The suprachoroid is a series of sheets of connective tissue which connect the chorioid with the sclera. Six to eight lamellae may overlies each other but they are fewer posteriorly. The cleft-like spaces between constitute the *perichoroidal space*. Two long posterior ciliary arteries pass through this space, but there are no intrinsic suprachoroidal blood vessels. It has, however, a plexus of nerves in the lamellae. Toward the ciliary body smooth muscle fibers appear over the surfaces of the suprachoroidal lamellae. These are arranged in flattened stellate masses which become numerous toward the ciliary body and finally join with the ciliary muscle. The perichoroidal space is regarded by some as a lymph space, by others as a bursa due to movement of the ciliary muscle in accommodation.

The *blood vessel layer* shows an outer layer of larger vessels and an inner layer of smaller ones, but with no distinct intervacular space between them. Arteries appear to be more abundant in the outer layer. They are derived from the short posterior ciliary arteries which penetrate the sclera around the entrance of the optic nerve and form a plexus in the vascular layer. These arteries have well developed muscle coats, including longitudinal fibers in the larger vessels. The veins are tortuous vessels without muscle in their walls, but surrounded by perivascular lymph sheaths. They converge into the *venae vorticosae*, two above and two below the equatorial plane, which drain the chorioid coat. The

connective tissue between the blood vessels contains flattened stellate pigmented cells. These *chromatophores* are closely associated with the blood vessels. The inner part of the blood vessel layer is made up of smaller vessels and capillaries, and by some is differentiated into a choriocapillary layer. In the eyes of many animals, as the ox and the horse, the posterolateral part of the chorioid, known as the *tapetum*, shows an iridescence, which is considered by some as aiding nocturnal vision. The iridescence is due to a marked fibrous condition of the zone between the blood vessels of the vascular layer (horse) or to many layers of flattened iridescent cells just outside the choriocapillary layer. The *supracapillary layer* lies between the layer of large blood vessels and the choriocapillary

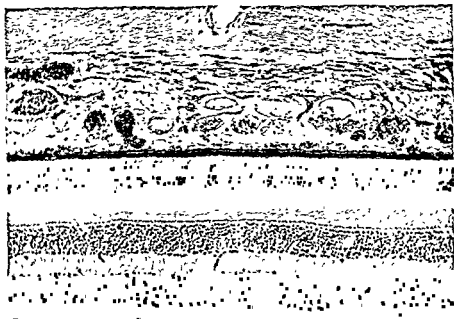


FIG 188—SECTION THROUGH THE LAYERS OF THE EYE NEAR THE MACULA REGION.
From Bremer, *Textbook of Histology*, P. Blakiston's Son & Co., Philadelphia, 1936

layer. It is made up of a feltwork of fibrils and stroma cells, and a chorioid *tapetum*.

The *basal membrane* or *Bruch's membrane* is a noncellular, highly refractile sheet about 1 micron thick, but increasing toward the optic nerve and toward the edge of the retina.

RETINA—The adult retina (Figs. 186, 188, 189 and 190) has an outer pigmented layer and an inner visual layer. External to the pigmented layer is a basal layer, upon which the hexagonal pigment cells rest. The free ends of these cells have pseudopodia-like processes which interdigitate with the rods and cones of the visual layer. The pigment cells have a diameter of about 16 microns and are about 8 microns tall. They are taller at the fovea. Each cell covers about nine cones in the fovea and a larger number of both rods and cones elsewhere in the retina. The extension and retraction of the pigmented processes

in relation to the amount of light entering the eye has been thoroughly studied in lower vertebrates by Arey. When much light enters the eye the processes extend so as to cover the rods and cones with pigment, thus reducing the stimulation to these neuro-epithelial structures. Under conditions of less light the processes retract, exposing the rods and cones. In man the migration of pigment is regarded as slight.

With ordinary histological methods the retina shows ten layers, including the pigmented layer. From without inward these are: (1) the pigmented epithelium; (2) rods and cones; (3) external limiting membrane; (4) outer nuclear or granular layer; (5) outer plexiform or molecular layer; (6) inner nuclear or granular layer; (7) inner plexiform or molecular layer; (8) ganglion cells; (9) nerve fibers; (10) internal limiting membrane.



FIG 189—VERTICAL SECTION OF BACILLARY LAYER OF RETINA OF A TWENTY-FOUR-YEAR-OLD MAN, IN THE REGION OF THE FOVEA CENTRALIS.

1, pigment layer; 2, rods and cones, the outer segment stained dark; 3, fiber baskets ("rod sockets"), comprising the terminal fibrils of Muller's fibers; 4, external limiting membrane, 5, nucleus of cone, 6, nucleus of rod visual cell. (Eisler.) From Jordan, *A Textbook of Histology*, 7th ed, D Appleton-Century Co., Inc., New York, 1937.

processes into layer 7 and their axons make up layer 9.

The supporting elements of the retina are neuroglial cells, in keeping with its derivation from the embryonic brain wall. The principal elements are the *radial fibers* or *fibers of Müller*. These are elongated cells extending from the internal limiting membrane to the external limiting membrane. The external membrane is formed by the fusion of the radial fibers in the tangential plane. The membrane is perforated with numerous openings through which the rods and cones project. The nuclei and processes of the neuro-epithelial cells lie

below the openings, in the outer nuclear and outer molecular layers. External to the membrane short processes extend from the Müller fibers to form fiber baskets about the rods and cones. The external membrane thus serves to hold the receptor elements in place.

The nuclei of the Müller fibers are found in the inner nuclear layer, among those of the bipolar cells. The Müller fibers are regarded as forming a syncytium in the retina, by branching and anastomosis of delicate processes which hold the various elements of the retina in place. The basal ends of the Müller fibers are cone shaped, with broad bases. The edges of these bases are attached

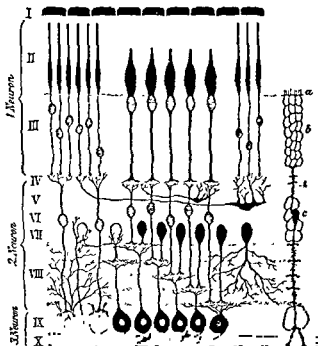


FIG. 190—SCHEMATIC SECTION OF THE HUMAN RETINA (Greeff).

I, pigmented epithelium, *II*, rod and cone layer; *III*, outer nuclear layer; *IV*, outer plexiform layer, *V-VII*, inner nuclear layer; *V*, horizontal cells, *VI*, bipolar cells; *VII*, amacrine cells; *VIII*, inner plexiform layer; *IX*, ganglion cell layer; *X*, nerve fiber layer. At the right is a Müller's fiber. From Cowdry, *Special Cytology*, Paul B. Hoeber, Inc., New York, 1932.

together to form the internal limiting membrane. In addition to the radial fibers of Müller there are neuroglia cells with horizontal branches. It will be noted that the neuroglial elements do not extend to the ends of the rods and cones or to the pigmented layer. In detachment of the retina separation occurs between the rods and cones and the pigment layer.

The *neuro-epithelial cells* are of two types, namely, *rods* and *cones*. They are the photoreceptors. Developmentally they represent the outer layer of cells of the optic placode, which, however, with the folding up of the neural tube, line the cavity of the optic vesicle. With further development they are brought into close relation with the pigmented layer.

in relation to the amount of light entering the eye has been thoroughly studied in lower vertebrates by Arey. When much light enters the eye the processes extend so as to cover the rods and cones with pigment, thus reducing the stimulation to these neuro-epithelial structures. Under conditions of less light the processes retract, exposing the rods and cones. In man the migration of pigment is regarded as slight.

With ordinary histological methods the retina shows ten layers, including the pigmented layer. From without inward these are: (1) the pigmented epithelium; (2) rods and cones; (3) external limiting membrane; (4) outer nuclear or granular layer; (5) outer plexiform or molecular layer; (6) inner nuclear or granular layer; (7) inner plexiform or molecular layer; (8) ganglion cells; (9) nerve fibers; (10) internal limiting membrane.

From the viewpoint of functional elements, however, there are only four layers, namely: (1) the pigmented layer, already described; (2) the neuroepithelial layer, including the rods and cones, with their cell bodies and processes; (3) the bipolar cells, which have dendritic processes synapsing with the processes of the rod and cone cells, on the one hand, and an axon tuft which synapses with the dendrites of the ganglion cells, on the other hand; (4) the ganglion cells, which collect stimuli from many bipolar cells and through their axons, forming the optic nerve, convey the stimuli to the brain. The neuroepithelial layer includes layers 2, 4, and part of 5, while the layer of bipolar cells includes the inner part of layer 5 and layer 6 and part of 7. The ganglion cells (layer 8) send their dendritic

FIG. 189.—VERTICAL SECTION OF BACILLARY LAYER OF RETINA OF A TWENTY-FOUR-YEAR-OLD MAN, IN THE REGION OF THE FOVEA CENTRALIS.

1, pigment layer; 2, rods and cones, the outer segment stained dark, 3, fiber baskets ("rod sockets"), comprising the terminal fibrils of Muller's fibers; 4, external limiting membrane, 5, nucleus of cone, 6, nucleus of rod visual cell. (Eisler) From Jordan, *A Textbook of Histology*, 7th ed., D. Appleton-Century Co., Inc., New York, 1937.

processes into layer 7 and their axons make up layer 9.

The supporting elements of the retina are neuroglial cells, in keeping with its derivation from the embryonic brain wall. The principal elements are the radial fibers or fibers of Muller. These are elongated cells extending from the internal limiting membrane to the external limiting membrane. The external membrane is formed by the fusion of the radial fibers in the tangential plane. The membrane is perforated with numerous openings through which the rods and cones project. The nuclei and processes of the neuro-epithelial cells lie

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do with color vision. The smaller diameter and greater crowding of cones in the fovea is regarded as related to the sharpness of vision in this part of the retina. The fovea has its greatest differentiation from the rest of the retina in the primates and especially in man.

The *bipolar cells* are nerve cells whose nuclei form the inner nuclear layer. They are divided into *centripetal* and *centrifugal* bipolars. The centripetal cells form the second link in transmission of visual stimuli from the rods and cones to the optic centers. There are large and small cells of this category. The large ones have a considerable spread of dendritic processes which make synaptic connections in the outer molecular layer with from ten to one hundred rod or cone cells. The small bipolars are connected with only one cone cell each, none of the rod cells effecting synaptic connections with this type. The large bipolars thus collect stimuli from many receptor cells, transmitting them to the ganglion cell dendrites in the inner molecular layer.

The centrifugal bipolar cells transmit impulses to the rods and cones, possibly regulating the excitability of these elements. They apparently receive their stimuli from the ganglion cells. They have been included under the term amacrine cells, but Poljak has demonstrated small axons extending to the bases of the rods and cones. The occurrence of true amacrine nerve cells in the retina is unsettled.

Horizontal cells have the function of collecting stimuli from groups of rod and cone cells by means of their horizontally spread dendritic processes. Their cell bodies and nuclei lie in the outer part of the inner nuclear layer. The dendrites extend into the outer molecular layer where they synapse with the rod and cone cells. The axons also extend horizontally within the outer molecular layer as a rule and end in relation to the rod and cone cells of other parts of the retina. The horizontal cells are to be regarded as association neurons.

The *ganglionic cells* are multipolar nerve cells whose dendritic processes extend into the inner molecular layer. Here they make synaptic connections with the bipolar cells. They form the third link in the path of the visual impulse. The axons of these cells form the optic nerve, carrying the impulse to the optic centers of the brain. These axons converge from all parts of the retina toward the head of the optic nerve. In their course over the retina they form the ninth or nerve fiber layer. This layer is thin at the retinal periphery where the fibers are relatively few, and becomes thick near the optic disc by the confluence of fibers. In their course over the retinal surface they are unmyelinated. They penetrate the lamina cribrosa and acquire a myelin sheath, but without a neurolemma. The optic nerve thus resembles a central fiber tract rather than a peripheral nerve, histologically as well as embryologically.

Fovea centralis Lateral to the papilla formed by the head of the optic nerve (the blind spot) there is a shallow depression with a diameter of about 1 mm. This is the *fovea centralis*. It lies in line with the center of the cornea. The retina is thinnest at the bottom of the fovea. Here the ganglion cells are present

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The *rod cells* are slender elements which are divided into an outer *rod* and an inner *rod fiber*. The rod fiber lies below the external limiting membrane, reaching the outer molecular layer. Here it ends as a small knob which gives off fine terminal processes. These form synaptic connections with processes of the layer of nerve cells. The rod fiber contains a granular cytoplasm and the nucleus is surrounded by a thin layer of cytoplasm and lies in the outer nuclear layer.

The rods project through perforations in the external limiting membrane as described and reach the pigmented layer of the retina. Save in a zone near the ora serrata the rods contain a pigment known as *rhodopsin* or *visual purple* which is acted upon by light. It has been regarded as undergoing a chemical change which excites nervous impulses in the rod cells. Experimental evidence indicates that it has to do with adaptation of the retina to different intensities of light. Regeneration of visual purple appears to occur only when the intimate relation of rods and the pigment epithelium is maintained.

The rods vary in length from 40 microns near the ora serrata to 60 microns near the fovea. They have a diameter of 2 microns. They outnumber the cones but do not have a uniform distribution. In the middle of the *fovea centralis*, the point of sharpest vision, the rods are absent. At the margin of the fovea the rods are found scattered among the cones. They gradually increase in number and in ratio to the cones, so that in the greater part of the retina there are three or four rods between each two cones. At the extreme periphery of the visual part of the retina the rods again become less in number. The total number of rods in the human retina is estimated by Poljak as 130,000,000.

The *cone cells* are also divided into two parts. The *cone fiber* is of larger diameter than the rod fiber. It varies in length, being long at the macula and short at the periphery of the retina. The nuclei of the cone cells are somewhat larger than those of the rods and are located just below the external limiting membrane. The cone fibers end in terminal feet in the outer molecular layer.

The outer segments or *cones* are flask-shaped structures varying in form and length. At the fovea they are slender elements somewhat resembling the rods, 2.5 microns in diameter and 85 microns long. Here they number about 4000 and are the only visual elements present. At the margin of the fovea the rods make their appearance and the cones become shorter and larger in diameter. In the fundus the cones are 7 microns broad and 32 microns long and at the periphery of the retina 7.5 microns broad and 22 microns long. The total number is estimated at 7,000,000. The cones have no visual purple.

There is evidence that the rods are more important for vision in dim light, the visual purple being regarded by some students of the eye as facilitating vision under such conditions. Many nocturnal animals have only rods in the retina and in others only rudimentary cones are present. In some diurnal forms, as many reptiles, only cones are found. Casey Woods has shown that in birds the cones outnumber the rods. It has been suggested that the cones have to

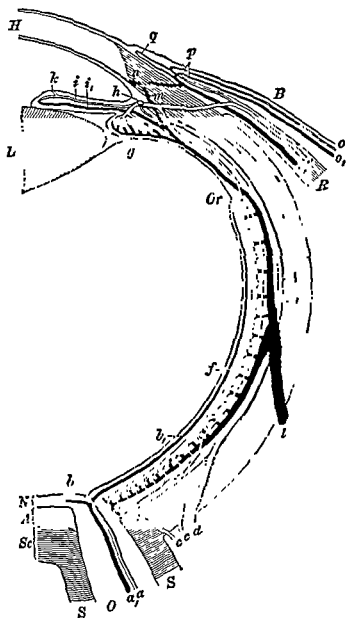


FIG 191—SCHEMATIC REPRESENTATION OF THE INTRINSIC BLOOD VESSELS OF THE EYE.

Arteries in outline, veins in solid black, *A*, choroid; *a*, central artery, and *a*₁, vein of the retina, *B*, conjunctiva; *b*, retinal arteries, *b*₁, retinal veins; *c*, *c*, short ciliary arteries; *d*, long ciliary artery, *c*, *c*₁, anterior ciliary arteries and veins; *f*, choriocapillaries; *g*, capillaries of the ciliary body; *H*, cornea; *h*, circulus major of the iridal arteries; *i*, arteries, and *i*, veins in the iris, *k*, circulus minor of the iridal arteries; *L*, crystalline lens; *l*, venae vorticosae, *m*, anastomosis of ciliary and anterior ciliary veins; *N*, retina; *n*, canal of Schlemm; *o*, optic nerve; *o*, posterior conjunctival artery, and *o*₁, vein, *p*, anterior conjunctival vessels, *q*, vascular loops at the margin of the cornea, *R*, internal rectus muscle; *S*, sheath of the optic nerve, *Sc*, sclera (After Leber.) From Jordan, *A Textbook of Histology*, D Appleton-Century Co., Inc, New York, 1937.

in a single layer and their axons diverge away from the fovea. Also fibers from other parts of the retina, on approaching it to reach the optic nerve, bend around it so as to leave the fovea uncovered. Since all the light which reaches the neuro-epithelial elements of the retina must pass through all of its layers, the arrangement in the fovea favors sharpness of vision.

The fovea and a little of the surrounding zone has a yellow color when fresh, in contrast to the red color of the remainder of the retina. This zone, including the fovea, is therefore called the *yellow spot (macula lutea)*. It is about 2 mm. in diameter and is located 3 mm. lateral to and slightly below the plane of the optic papilla. The yellow color is due to a pigment which is more resistant to light than is the visual purple.

BLOOD SUPPLY (Fig. 191).—The retina receives its blood supply from the central artery of the optic nerve. This branches within the retina but there are no capillaries external to the outer molecular layer. There is some anastomosis in the region of the lamina cribrosa with the posterior ciliary artery, but aside from this, there is no other source of supply to the retina. These anastomoses are usually merely capillary or precapillary vessels so that functionally the central artery is a terminal artery. The central vein follows the artery.

The *space of Tenon* can be injected by introducing the injection mass between the sclera and the chorioid coat, the mass finding its way along the walls of the vortical veins. This space can also be injected from the subarachnoid space surrounding the brain.

The *aqueous humor* which is secreted or transuded by the ciliary processes passes first into the posterior chamber. It may then pass to the vitreous body, or forward through the pupil to the anterior chamber. It is drained through the *spaces of Fontana*, at the angle of the iris, into the canal of Schlemm.

Aside from the optic nerve the eyeball is supplied by the *ciliary nerves*. Sensory fibers from the ophthalmic nerve supply the cornea and ocular conjunctiva. Cranial autonomic fibers from the ciliary ganglion supply the ciliary muscle and the constrictor fibers of the iris. Thoracolumbar autonomic fibers from the superior cervical ganglion supply the radial smooth muscle fibers of the iris.

CENTRAL CONNECTIONS

The **OPTIC NERVE**, as already stated, corresponds to a fiber tract of the brain. It is covered with a dural membrane continuous with the dura mater of the brain. The immediate covering of the nerve corresponds to the pia. Between these two layers is a space, corresponding to the subarachnoid space, which has some loose connective tissue. The supporting elements of the optic nerve itself are neuroglia. They hold the nerve fibers together in bundles.

The nerve fibers number about 1,200,000, and are derived from a similar number of ganglion cells in the retina. The ratio of fibers to rods and cones varies for different parts of the retina, the average being one fiber for each

100 rod and cone cells. At the fovea, however, there is one fiber for each cone cell.

As already stated the myelin sheaths of the optic fibers normally are discontinued at the lamina cribrosa, so that the diameter of the nerve is greatly reduced at the papilla. Occasionally myelin extends into the interior of the eye, thus increasing the size of the blind spot. The optic nerve does not regenerate when severed.

The OPTIC CHIASMA is formed by the crossing of optic nerve fibers. Those from the medial half of each retina cross, while those from the lateral half remain uncrossed. The latter, with the crossed fibers from the opposite side, form the so-called optic tracts. In animals with less overlapping of the fields of vision than in man, a smaller proportion of the optic fibers remain uncrossed. According to Craigie the proportion in the rat is about 20 per cent.

The OPTIC TRACT contains, in addition to optic fibers, crossed and uncrossed, the *commissure of Gudden*. This connects the nonoptic medial geniculate bodies of the two sides, its upper portion constituting the *medial root* of the optic tract. Optic fibers to the lateral geniculate body, the superior colliculus and the pretectal region form the larger *lateral root*.

The fibers from the upper quadrants of the retina become so arranged in the formation of the optic nerve as to lie above those of the lower quadrants. Likewise those from the lateral quadrants lie lateral to the medially derived fibers. In the optic chiasma the upper quadrant fibers cross dorsally and the ventral quadrant fibers cross ventrally. In the optic tract the fibers from the upper quadrants of both retinae assume a dorsomedial position and those from the lower quadrants take a ventromedial position.

The fibers from the macula appear to lie between the upper and lower quadrant fibers in the optic nerve. They cross chiefly in the middle of the chiasma. In the optic tract the macular fibers constitute the dorsolateral portion of the tract and overlap the upper and lower quadrant fibers medioventrally.

Brouwer and Zeeman have shown that the upper quadrant fibers terminate medially in the lateral geniculate body and the lower quadrant fibers terminate laterally. The macular fibers spread throughout the nucleus, making synaptic connections with more neurons than do the others.

The OPTIC RADIATION (Fig. 193) according to Poljak, arises entirely from the lateral geniculate body. Brouwer found no optic fibers to the pulvinar, but Walker and Le Gros Clark found chromatolysis in the pulvinar *after lesions* in the occipital cortex. The optic radiation extends through the caudal part of the internal capsule to the *striate area* of the occipital lobe. This is the cortical area of conscious vision. According to Poljak's results in primates the adjacent areas receive no fibers from the primary optic centers.

The results of Brouwer's studies indicate that geniculocortical fibers from the lower medial part of the lateral geniculate body pass to the *cuneus*, above the calcarine fissure. Fibers from the lower lateral portion of the geniculate

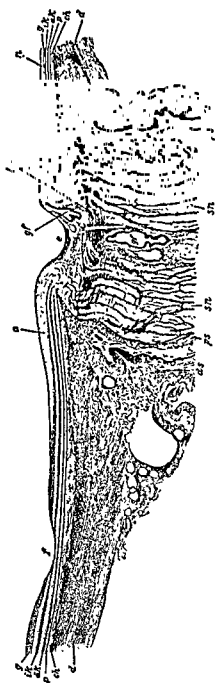


FIG. 192.—ENTRANCE OF THE OPTIC NERVE.

ak, outer granular layer of the retina; *ch*, choroid coat; *d*, sclera; *ds*, dural sheath; *e*, depressed center of the optic papilla; *f*, fovea centralis; *g*, layer of ganglion cells; *gf*, blood vessels; *ik*, inner granular layer; *lcr*, lamina cribrosa; *n*, nerve fiber layer; *p*, pigment layer; *ps*, pial sheath; *sn*, funiculi of optic nerve fibers. X 27. (After Kölliker.) From Jordan, *A Textbook of Histology*, D. Appleton-Century Co., Inc., New York, 1937.

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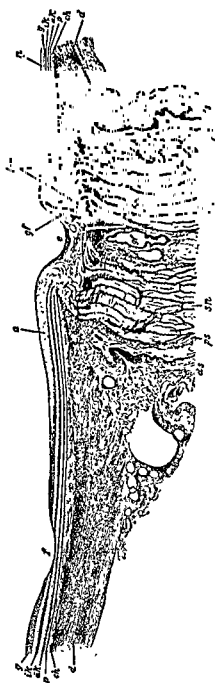


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body end in the *lingual gyrus* below the calcarine fissure. The fibers which relay macular vision have an intermediate position in the optic radiations and

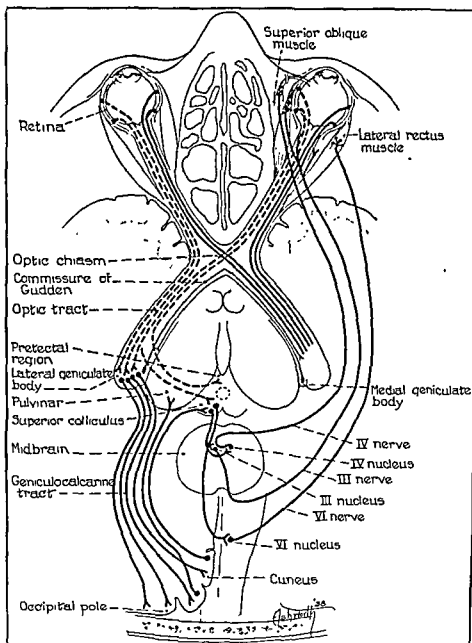


FIG. 193—OPTIC VISUAL AND REFLEX PATHS.

are projected onto the posterior third of the visual cortex, both above and below the calcarine fissure (Fig. 194).

Included in the optic radiations are *corticofugal fibers* which end in the superior colliculus and in the nuclei of the pons.

THE OPTIC SYSTEM

REFLEX CONNECTIONS (Fig. 193).—The *superior colliculus* receives optic fibers from the lateral root of the optic tract. According to the experimental results of Magoun (1933) and Magoun and Ranson (1935) the superior colliculus has to do with reflex movements of the head and eyes in response to visual stimuli. A tectospinal tract extends to the upper cervical segments of

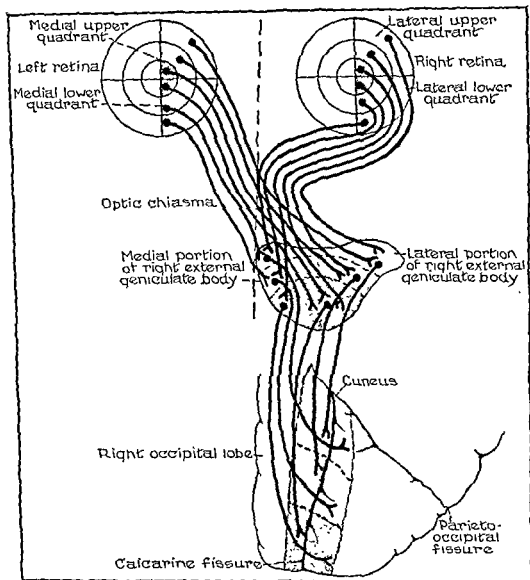


FIG. 194.—PROJECTION OF RETINAL FIELDS ON VISUAL CORTIX.
Modified after Rasmussen

the cord. Functionally this appears to be supplemented by a crossed tectobulbar tract which relays in the reticular formation of the medulla oblongata to the reticulospinal tract, which extends to the lower part of the cord. There is also a reflex pathway from the superior colliculus to the eye muscle nuclei through the medial longitudinal bundle.

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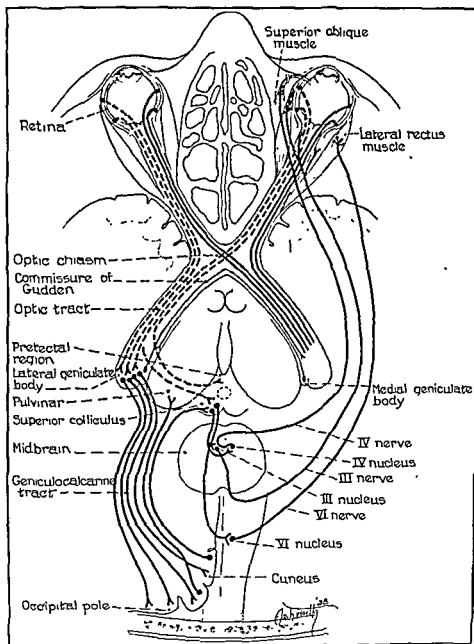


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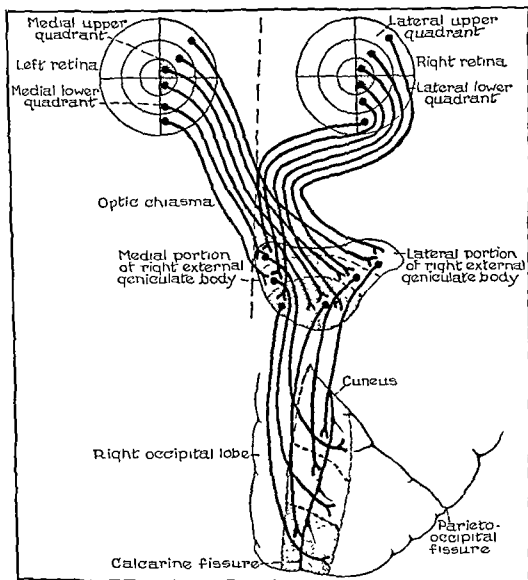


FIG. 194—PROJECTION OF RETINAL FIELDS ON VISUAL CORTEX.
Modified after Rasmussen

the cord. Functionally this appears to be supplemented by a crossed tectobulbar tract which relays in the reticular formation of the medulla oblongata to the reticulospinal tract, which extends to the lower part of the cord. There is also a reflex pathway from the superior colliculus to the eye muscle nuclei through the medial longitudinal bundle.

Pupillary reflexes to increased light are brought about by optic fibers which enter the *pretectal region*, a transition zone between thalamus and tectum. From cells in this zone the impulses are relayed to the nucleus of Edinger and Westphal, which gives rise to the preganglionic cranial autonomic fibers of the IIIrd nerve. The impulses are relayed in the ciliary ganglion to fibers which end in the circular smooth muscle fibers of the iris. These contract on stimulation, thus reducing the size of the pupil.

Dilatation of the pupil is brought about by impulses through tectospinal fibers to the upper thoracic segments of the cord. From cells in the intermediolateral horn they are relayed through preganglionic fibers of the thoracolumbar autonomic system to the superior cervical ganglion. Cells in this ganglion give rise to fibers which reach the radial muscles of the iris via the internal carotid plexus and the short and long ciliary nerves. Impulses over this reflex pathway produce dilatation of the pupil.

CLINICAL INTERPRETATION

LESIONS IN THE OPTIC PATHWAY

A lesion of one optic nerve produces blindness in the corresponding eye.

A lesion in the lateral part of the optic chiasma on one side or the other results in blindness in the nasal visual field of the corresponding eye (*unilateral nasal hemianopsia*). This is due to interruption of the non-decussating fibers, which are situated in the lateral part of the chiasma.

A lesion in the central part of the optic chiasma results in blindness of the outer half of the visual fields of both eyes (*bitemporal hemianopsia*). This is due to interruption of the decussating fibers from both retinae which carry impulses derived from the temporal fields of vision. The field defects are usually irregular, due to a larger number of fibers from one eye being involved than from the other.

A lesion of the right optic tract between the chiasma and the lateral geniculate body results in blindness in the left field of vision of both eyes (*left sided hemianopsia*) or vice versa. Since the decussating fibers from each eye serve its lateral field of vision and the non-decussating fibers serve the nasal field of vision of that eye, the entire visual field, right or left, will be lost if one or the other optic tract is destroyed.

Lesions in the occipital lobe, if limited to an area above the calcarine fissure, cause blindness in the opposite lower quadrants of both visual fields, e.g., a lesion of the left cuneus produces blindness in the right lower quadrant of the visual field. Lesions in the lingual gyrus, below the calcarine fissure, result in blindness in the opposite upper quadrants of the visual fields.

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CHAPTER 21

THE OLFATORY APPARATUS

and

RHINENCEPHALON

ORGAN OF SMELL

The sensory organ of smell is the *olfactory membrane* (Figs. 195 and 196), forming a yellowish-brown area in the upper part of the nasal cavity. It comprises a zone of very irregular outline on the middle upper third of the nasal septum and the adjacent superior concha on each side. The total area of the two sides has been estimated as 500 sq. mm. The membrane consists of a tunica propria and olfactory epithelium.

The epithelium consists of three kinds of cells, namely, olfactory, supporting and basal. The *olfactory cells* are the receptor elements. Their free ends project to the surface through openings in the cuticular membrane, forming small *olfactory vesicles*. Each vesicle has 6 to 8 fine cilia, 2 microns long. The nuclei of the olfactory cells are rounded and are arranged in many layers, forming a broad zone in the epithelium. The basal ends of these cells continue as nerve processes which enter the olfactory bulb. The *sustentacular* or *supporting cells* are tall, nonciliated, epithelial elements with oval nuclei. The free surfaces form cuticular plates held together by terminal bars. The outer halves of these cells contain the yellowish pigment which gives color to the olfactory membrane. The lower halves branch and form a network. The *basal cells* lie between the bases of the supporting cells as a single layer. They have dark staining nuclei and branching processes.

The *tunica propria* of the olfactory membrane is made up of fibrous tissue and elastic fibers and is continuous with the underlying periosteum. It contains the *olfactory glands* of Bowman. These are branched, tubulo-alveolar glands of serous type, formed of cubical or low pyramidal cells containing secretory granules. The secretion of the glands bathes the olfactory epithelial surface. It is believed to dissolve the minute particles of substance which give rise to olfactory stimuli and to facilitate stimulation of the olfactory cells. It has been suggested that solution and concentration of such substances are facilitated by colloids probably contained in the secretion and in connection with the olfactory hairs.

The olfactory nerve (Fig. 197) is made up of the numerous fibers from the

THE OLFACTORY APPARATUS

cells above described. The fibers become arranged into small bundles which are aggregated into about 20 larger bundles on each side. These pass through the small foramina in the cribriform plate to reach the olfactory bulb.

The olfactory organ belongs to the group of chemoreceptors. It is extremely sensitive but is also easily fatigued. In man the entire olfactory apparatus is greatly reduced as compared with most of the mammals.

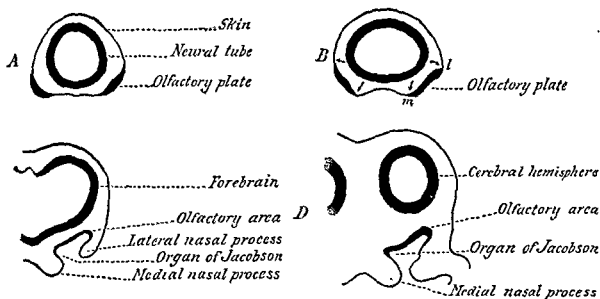


FIG 195.—DEVELOPMENT OF THE OLFACTORY ORGAN, AS SHOWN BY TRANSVERSE SECTION THROUGH THE HEAD.

A, early olfactory placodes in embryo of 5 mm *B*, olfactory placode and beginning nasal processes (*m* and *l*) in embryo of 6.5 mm *C*, showing olfactory fossa in embryo of 9 mm. *D*, showing further differentiation of olfactory fossa in embryo of 10 mm. From Jackson-Morris, *Human Anatomy*, P. Blakiston's Son & Co., Philadelphia, 1933.

RHINENCEPHALON

The rhinencephalon (Fig. 197) includes the various portions of the cerebral hemispheres which have to do with the olfactory system. These are: (1) the olfactory bulb, (2) the olfactory tract, (3) the olfactory trigone, olfactory tubercle and pyriform area, (4) the paraterminal area, (5) the hippocampal formation, and (6) the fornix. They are widely separated in the human brain.

The forebrain of fishes is largely an olfactory reflex center with no cerebral cortex. In amphibians the cortex has its inception as a new structure derived from olfactory centers. In reptiles the olfactory cortex is well marked, with a definite but simple histological pattern. A nonolfactory cortex also makes its appearance. In the evolution of the forebrain the olfactory cortex or archicortex has become overshadowed by the neocortex which receives impulses derived from optic, acoustic, tactile and other senses. The neocortex reaches its maximum development in the human brain, overshadowing all the rhinencephalon.

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THE OLFACTORY APPARATUS

OLFACTORY TRACT.—The axons of the mitral cells pass into the nerve fiber layer and turn posteriorly as the olfactory tract. Axons of the tufted cells also enter the fiber layer. They cross in the anterior commissure, to enter the opposite olfactory bulb through its olfactory tract. The olfactory tract is thus composed of coarse efferent fibers from the mitral cells and of fine efferent

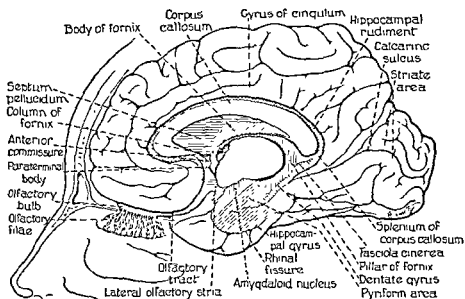


FIG. 107.—MEDIAL VIEW OF BRAIN SHOWING OLFACTORY NERVE AND BULB AND SOME OLFACTORY PARTS OF THE BRAIN.

fibers from the tufted cells of the same side. In addition it contains fine afferent fibers from the tufted cells of the opposite olfactory bulb. The axons of the mitral cells pass to the secondary olfactory centers. The tract occupies the olfactory furrow on the underside of the frontal lobe. On reaching the peduncle

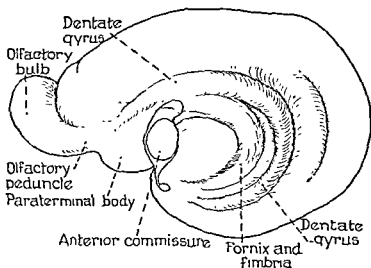


FIG. 108.—MEDIAL VIEW OF BRAIN OF A MARSUPIAL SHOWING OLFACTORY PARTS OF THE BRAIN. Redrawn from Elliot Smith.

In lower mammals and in the human fetus the various centers of the olfactory apparatus lie relatively close together. The expansion of the cortex and the growth of the thalamus, together with the wedging action of the corpus callosum as it increases in size from lower to higher mammals, have brought about a separation of the centers. The rearrangement of the brain surface associated with the development of the lobes of the hemisphere, especially the temporal, has greatly altered the positions of the olfactory centers in the adult human brain.

The OLFACTORY BULB is a flattened ovoid mass of gray substance constituting the primary olfactory center. In the adult it is solid, but in many mammals and in the human embryo an extension of the lateral ventricle forms

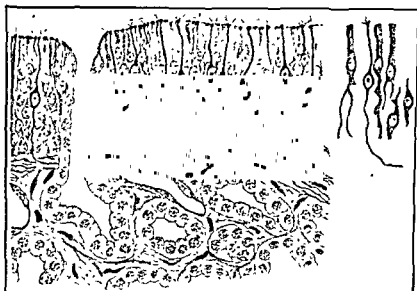


FIG. 196—OLFACTORY EPITHELIUM OF CALF.

The olfactory cells contrast sharply with the more numerous sustentacular cells. (Hardesty.) From Jordan, *A Textbook of Histology*, D. Appleton-Century Co, New York, 1937.

a cavity in the bulb. The position of this cavity is marked by a central ependymal mass. The olfactory bulb is classified by Brodmann with his *cortex primitivus*, which has no functional lamination. However, several histological zones can be recognized. The outer zone on the underside is an interlacing mass of olfactory nerve fibers which enter the bulb. Penetrating deeper they terminate in tufts in relation to telodendrites of large cells, the *mitral cells*, and of smaller *tufted cells*. The synaptic terminal branches form rounded masses known as *glomeruli*. Within the glomeruli are described small nerve cells and neuroglia. The axons of the nerve cells bring neighboring glomeruli into relation with each other. Deeper than the glomeruli is a layer of tufted cells and then a layer of mitral cells. The mitral cells have long, wide-spreading dendrites. Most of them end in the glomeruli but some end in relation to branches of the tufted cells.

THE OLFACTORY APPARATUS

the inferior surface of the uncus and is lost on the medial surface. The *rhinal fissure* continues posteriorly as the boundary between pyriform area and neo-cortex. The pyriform area is a secondary olfactory center, receiving fibers which arise from the mitral cells of the olfactory bulb. It relays impulses to the hippocampal formation.

The HIPPOCAMPAL FORMATION is made up of olfactory structures along the medial margin of the pallium. It includes the hippocampus, the dentate gyrus, the supracallosal gyrus, the longitudinal stria, the subcallosal gyrus and the diagonal band of Broca. Fibers from the pyriform area pass posteriorly and medially to the medial margin of the pallium. Here is formed a mass of gray substance known as the dentate gyrus (*fascia dentata*) which is a tertiary

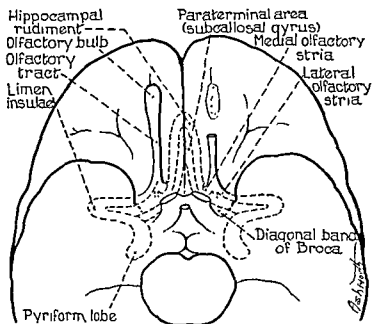


FIG 200—VENTRAL VIEW OF BRAIN SHOWING OLFACTORY STRUCTURES.

olfactory center. The dentate gyrus curves upward and posteriorly to become continuous below the splenium of the corpus callosum with the reduced *fasciola cinerea*. This continues into a thin layer of gray substance, the rudimentary *supracallosal gyrus* or *indusium griseum*, which covers the corpus callosum. This in turn is continuous rostrally with the *subcallosal gyrus*. Two bands of myelinated fibers are superimposed on the *indusium griseum*, forming the *medial* and the *lateral longitudinal striae*. They are also known as the *striae Lancisii*. The lateral longitudinal stria passes to the *fasciola cinerea* and the dentate gyrus. The medial stria connects the subcallosal gyrus in front with the *fasciola cinerea*.

The HIPPOCAMPUS (AMMON'S HORN) is a submerged gyrus forming the greater part of the olfactory cortex. It forms a curved structure in the floor

of attachment to the brain it divides into lateral, intermediate and medial striae. These pass to the lateral, intermediate and medial olfactory areas, respectively.

The INTERMEDIATE OLFACTORY AREA lies between and behind the lateral and medial striae, which are the chief olfactory tracts. The *olfactory trigone* is a small triangular area between the lateral and medial olfactory striae. The *olfactory tubercle* or *parolfactory area of Broca* is a rudimentary structure immediately posterior and lateral to the trigone. When developed enough to be visible, it forms a small oval swelling. The *anterior perforated substance*, so-called because penetrated by numerous small blood vessels, is an area of gray matter on the ventral side of the brain in front of the optic chiasma. The intermediate olfactory stria enters it.

The LATERAL OLFACTORY STRIA passes to the pyriform area (Figs. 199 and 200) and the amygdaloid nucleus. The pyriform area includes the lateral olfac-

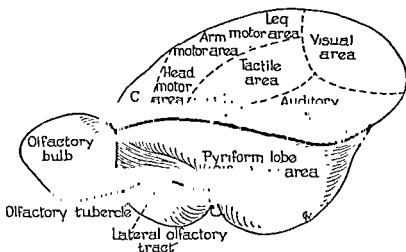


FIG. 199—LATERAL VIEW OF BRAIN OF A MARSUPIAL, SHOWING OLFACTORY PARTS OF BRAIN Redrawn from Elliot Smith.

tory gyrus, the uncus of the hippocampus, the anterior part of the hippocampal gyrus and the band of Giacomini. It is divided into anterior and posterior parts.

The LATERAL OLFACTORY GYRUS or anterior part of the pyriform area is separated from the neocortex by the rhinal fissure. It continues laterally, accompanied by the lateral olfactory stria on its medial border, into a deep cleft, the lateral cerebral fossa. This lies between the temporal lobe and the orbital part of the frontal lobe. The gyrus reaches the insula, forming the *limen insulae* (threshold of the insula). Here it is bent medially and backward at a sharp angle to reach the cerebral surface again on the underside of the temporal lobe. It is continuous with the upper lateral part of the uncus, which belongs to the posterior part of the pyriform area. The band of Giacomini is a continuation of the dentate fascia of the hippocampal formation which passes over

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the inferior surface of the uncus and is lost on the medial surface. The *rhinal fissure* continues posteriorly as the boundary between pyriform area and neo-cortex. The pyriform area is a secondary olfactory center, receiving fibers which arise from the mitral cells of the olfactory bulb. It relays impulses to the hippocampal formation.

The HIPPOCAMPAL FORMATION is made up of olfactory structures along the medial margin of the pallium. It includes the hippocampus, the dentate gyrus, the supracallosal gyrus, the longitudinal stria, the subcallosal gyrus and the diagonal band of Broca. Fibers from the pyriform area pass posteriorly and medially to the medial margin of the pallium. Here is formed a mass of gray substance known as the dentate gyrus (*fascia dentata*) which is a tertiary

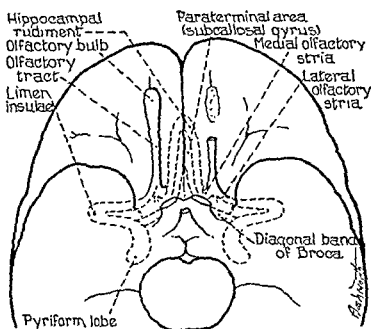


FIG. 200.—VENTRAL VIEW OF BRAIN SHOWING OLFACTORY STRUCTURES.

olfactory center. The dentate gyrus curves upward and posteriorly to become continuous below the splenium of the corpus callosum with the reduced *fasciola cinerea*. This continues into a thin layer of gray substance, the rudimentary *supracallosal gyrus* or *indusium griseum*, which covers the corpus callosum. This in turn is continuous rostrally with the *subcallosal gyrus*. Two bands of myelinated fibers are superimposed on the *indusium griseum*, forming the *medial* and the *lateral longitudinal striae*. They are also known as the *striae Lancisii*. The lateral longitudinal stria passes to the *fasciola cinerea* and the dentate gyrus. The medial stria connects the subcallosal gyrus in front with the *fasciola cinerea*.

The HIPPOCAMPUS (AMMON'S HORN) is a submerged gyrus forming the greater part of the olfactory cortex. It forms a curved structure in the floor

of the inferior horn of the lateral ventricle. It is also known as the hippocampus major, in contrast to the hippocampus minor or calcar avis, an elevation in the floor of the posterior horn of the lateral ventricle. It is continuous laterally with the hippocampal gyrus, which is a convolution of the cerebral cortex between the hippocampal and collateral fissures. The zone of transition between the hippocampal cortex and the hippocampal gyrus is known as the subiculum. It borders on the hippocampal fissure. The anterior end of the hippocampal gyrus is curved medially forming a hook of gray substance known as the *uncus*. This part of the gyrus is included with the archipallium, belonging to the pyriform lobe. The remainder is transitional to neopallium.

The cells of the hippocampus are large and numerous. They give rise to fibers which collect on its ventricular surface to form the *alveus*, which is a thin band

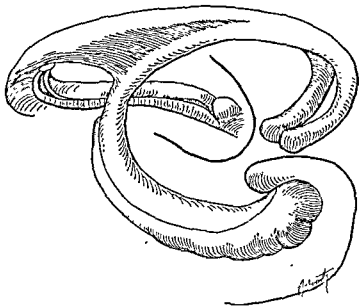


FIG. 201.—THE FORNIX AND HIPPOCAMPAL COMMISSURE.
Redrawn from Spitzka

of white substance Continuing toward the margin of the dentate gyrus and turning parallel to the edge of the pallium these fibers pass into the fimbria.

FORNIX AND FIMBRIA.—The *fornix* (Fig. 201) is a band of white substance under the corpus callosum extending from the fimbria to the mammillary bodies. The *fimbria* is a band of fibers which runs parallel to the dentate gyrus as far as the splenium of the corpus callosum. Here it turns forward as the *crus of the fornix*, the splenium of the corpus callosum serving to wedge it apart from the gyrus dentatus. Most of the fibers pass downward as a rounded vertical bundle, the *pillar of the fornix*. This passes through the hypothalamus to the mammillary body. Other fibers of the fimbria take part in forming the *hippocampal commissure* which passes beneath the posterior part of the corpus callosum to the opposite crus of the fornix. The fornix constitutes the efferent

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tract from the hippocampus to the brain stem and from the hippocampus of one hemisphere of the brain to the other.

The HIPPOCAMPAL GYRUS, according to Cajal, has a thick molecular layer of olfactory root fibers, a superficial layer of polymorphic cells, a layer of pyramidal cells and a deep polymorphic layer (Fig. 204). The *subiculum*, which is the part of the hippocampal gyrus next to the dentate fissure, has a superficial

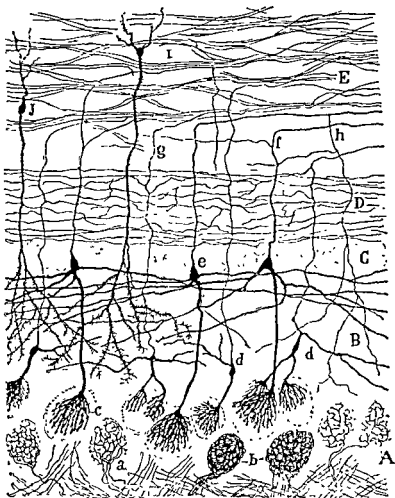


FIG. 202.—SECTION OF OLFACTORY BULB OF CAT SHOWING GLOMERULI, MITRAL CELLS AND TUFTED CELLS. GOLGI METHOD (From Cajal)

A, glomerular layer; *B*, external plexiform layer; *C*, layer of mitral cells; *D*, internal plexiform layer; *E*, layer of granules and white substance; *I*, *J*, internal granules; *a*, terminal tuft of an olfactory fiber; *b*, glomeruli formed of many olfactory tufts; *c*, dendritic tuft of a mitral cell; *d*, tufted cells, *h*, recurrent collateral from axon of a mitral cell

covering of myelinated nerve fibers. Below this are found three layers, namely, a molecular layer, a pyramidal layer and a polymorph layer. The deep white matter of the subiculum is a thick mass continuous with the alveus. The *pre-subicular region* is a transitional zone between subiculum and hippocampus proper. It does not receive direct olfactory fibers, but fibers from the olfactory cortex pass into it. It is regarded as an association center for olfactory sense.

The hippocampus proper has three layers above the *alveus* or layer of white matter. These are a fibrous layer, receiving fibers from pyramidal cells, and a layer of cells, rather large and fusiform, with a few lateral dendrites whose axons reach the alveus. There are also some small cells with short axons (Golgi type II) and a polymorph layer of cells whose axons mostly go to the alveus, but with Martinotti cells whose axons ascend to the molecular layer of the cortex. The alveus, or white matter of the hippocampus, is a thin layer of fibers from the pyramidal cells and from the pyriform area.

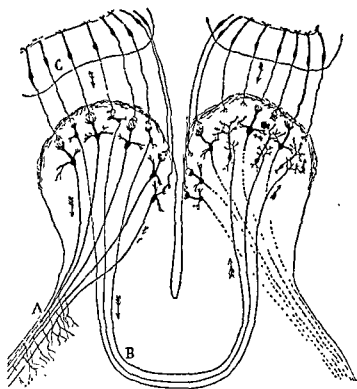


FIG. 203—SCHEMA OF THE COURSE OF THE OLFACTORY IMPULSE. (From Cajal.)

A, lateral olfactory stria, with collaterals; *B*, anterior fibers of anterior commissure; *C*, olfactory neuro-epithelial cells.

The *dentate gyrus* or *fascia dentata* (Figs. 197 and 204) is a strip of gray substance under the inner border of the hippocampus, receiving its name from tooth-like elevations on its medial border. It is the most primitive part of the hippocampus, and is composed of three layers, namely, a molecular layer of ovoid cells giving off axons, many of which bifurcate and pass in two directions, and a layer of polymorphs. The fibers from the cells of the dentate gyrus pass into the hippocampus and the fimbria.

The hippocampus and fascia dentata have afferent, efferent and commissural fibers. The afferent fibers arise from the pyriform lobule and form a bundle

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which ends in the molecular layer of hippocampus and fascia dentata. The efferent fibers pass into the fimbria of the fornix. There are two kinds, large and small. The large ones appear to be projection fibers, the small ones are commissural, passing in the hippocampal commissure to the fimbria and the hippocampus of the opposite side. The fornix thus is the efferent tract from the hippocampus to the brain stem and to the opposite side.

The AMYGDALOID NUCLEUS, which is an olfactosomatic center under the tip of the temporal lobe, also has connections from the lateral olfactory stria (Fig. 206), the latter reaching the medial part of the nuclear complex. This nuclear

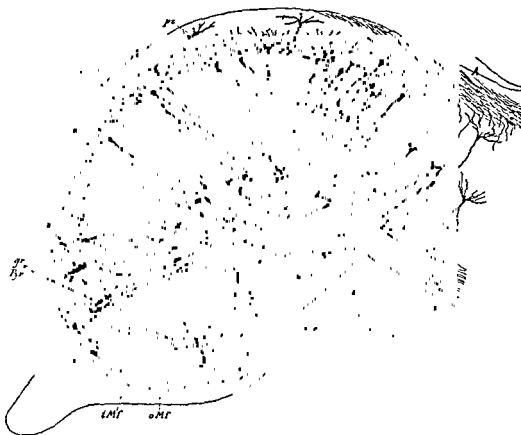


FIG. 204.—THE HIPPOCAMPUS AND DENTATE GYRUS OF A KITTEN GOLGI METHOD

A, alveus, *G.A.*, layer of axons of granule cells; *gr. Pyr.*, large pyramidal cells with processes to dentate fascia, *Kr*, granule cells with radial dendrites, *Mf*, principal bundle of mossy fibers, *oMf*, superficial layer of mossy fibers; *Plc*, intercellular plexus of the pyramidal cells, *Pyr*, pyramidal cells of dorsal fold of hippocampus; *pz*, polymorphic cells of the hippocampus; *Str.rad gr.*, stratum radiatum of dentate fascia; *Str.z S.*, stratum zonale of the subiculum; *IMf*, deep layer of mossy fibers. (From Koelliker)

mass also connects with the cortex of the pyriform lobe, with the hippocampus through the diagonal band of Broca, and with the olfactory tubercle and subcallosal gyrus. Its main efferent tract is the stria terminalis to the habenulae.

The hippocampus proper has three layers above the *alveus* or layer of white matter. These are a fibrous layer, receiving fibers from pyramidal cells, and a layer of cells, rather large and fusiform, with a few lateral dendrites whose axons reach the alveus. There are also some small cells with short axons (Golgi type II) and a polymorph layer of cells whose axons mostly go to the alveus, but with Martinotti cells whose axons ascend to the molecular layer of the cortex. The alveus, or white matter of the hippocampus, is a thin layer of fibers from the pyramidal cells and from the pyriform area.

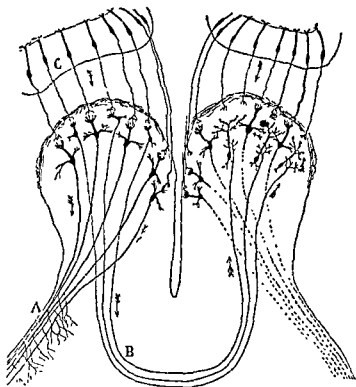


FIG. 203—SCHEMA OF THE COURSE OF THE OLFACTORY IMPULSE. (From Cajal.)

A, lateral olfactory stria, with collaterals; B, anterior fibers of anterior commissure; C, olfactory neuro-epithelial cells.

The *dentate gyrus* or *fascia dentata* (Figs. 197 and 204) is a strip of gray substance under the inner border of the hippocampus, receiving its name from tooth-like elevations on its medial border. It is the most primitive part of the hippocampus, and is composed of three layers, namely, a molecular layer of ovoid cells giving off axons, many of which bifurcate and pass in two directions, and a layer of polymorphs. The fibers from the cells of the dentate gyrus pass into the hippocampus and the fimbria.

The hippocampus and fascia dentata have afferent, efferent and commissural fibers. The afferent fibers arise from the pyriform lobule and form a bundle

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The MEDIAL OLFACTORY AREA (Fig. 205) includes the *subcallosal gyrus* (*paraterminal area*) and the *parolfactory area*. It receives the *medial stria*. It is connected with lower centers of the brain stem through the *olfactotegmental tract*, which gives collaterals to the nuclei of the tuber cinereum. There are also connections with olfactosomatic centers through the *medullary stria* of the thalamus to the habenular nucleus. From the latter the habenulopeduncular bundle relays impulses to the interpeduncular ganglion. Through the longitudinal striae the medial area connects with the cortex of the dentate gyrus and of the hippocampus. Fibers are also described as passing backward through the fornix to the dentate gyrus and the hippocampus. Fibers also arch through the septum pellucidum and penetrate the corpus callosum to reach the lateral and medial longitudinal striae. They are then distributed with the latter to the dentate gyrus and hippocampus.

CLINICAL INTERPRETATION

UNCINATE FITS

Lesions of the uncinate gyrus may result in *uncinate fits*. These are attacks during which the patient experiences sensations of olfactory stimuli, usually disagreeable odors. These sensations, which are olfactory hallucinations, are followed by a dreamy state of unreality. There may be various other sensory accompaniments, especially of taste. Motor phenomena may also appear, such as champing of the jaws and smacking of the lips.

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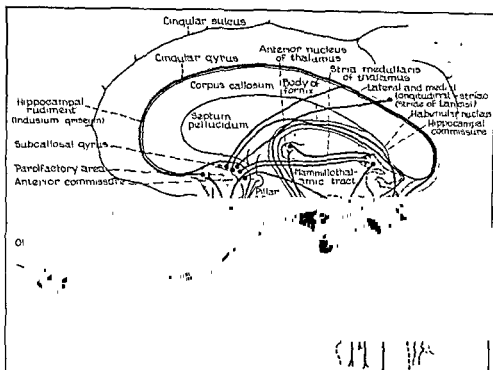


FIG. 205.—CONNECTIONS OF THE MEDIAL OLFACTORY CENTERS.

Modified after Rasmussen.

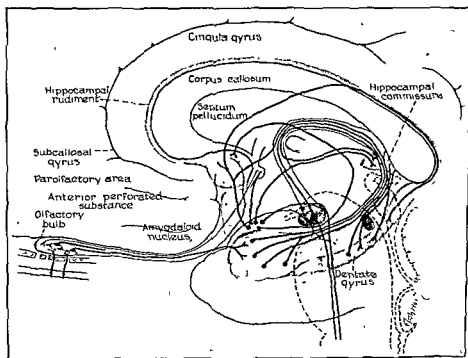


FIG. 206.—CONNECTIONS OF THE LATERAL OLFACTORY CENTERS.

Modified after Rasmussen.

STRUCTURE OF CEREBRAL CORTEX

nated fibers to and from the cortex; (4) in the relative time at which the fibers become myelinated after birth, and (5) in the types of cells.

Microscopic studies have been based on two types of preparations, namely, those stained to show myelinated fibers and those stained to show cell types and arrangement. By noting the relative coarseness or fineness of fibers and the number of vertical myelinated fibers entering and leaving the gray matter, in conjunction with the study of cell layers, Campbell has mapped out the

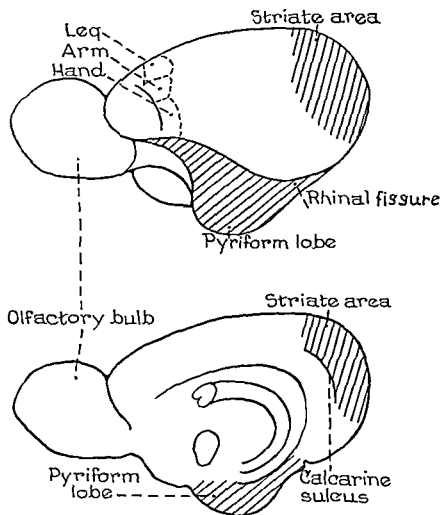


FIG 208.—DIAGRAM OF AREAS OF CORTEX IN PRIMITIVE MAMMAL.

Redrawn from G. Elliot Smith.

cortex into a number of fields. Adjacent areas of different structure are usually rather sharply marked off from each other, the boundary frequently being a sulcus or fissure. Sometimes, however, the boundary is at the convexity of a gyrus. On the basis of relative date of myelinization Flechsig has mapped out 36 chronological areas, subdivided into *primary*, *intermediate* and *late* groups. The *primary areas* are myelinated at birth or shortly after. They include chiefly the projection of fibers of the motor cortex and the visual, acoustic and olfac-

CHAPTER 22

STRUCTURE OF CEREBRAL CORTEX

The cerebral cortex is a layer of gray matter covering the cerebral hemispheres. The average thickness is usually given as 2.5 mm. but it varies from 4 mm. in the precentral gyrus to about 2 mm. in the occipital lobe. The total area is between about 200,000 and 248,000 sq. mm. The weight is about 580 grams. Economo gives the number of cells as thirteen billion six hundred fifty-three million.

The studies of Campbell, Elliot Smith, Brodmann, and others have shown that the cerebral cortex has different patterns of structure in different areas

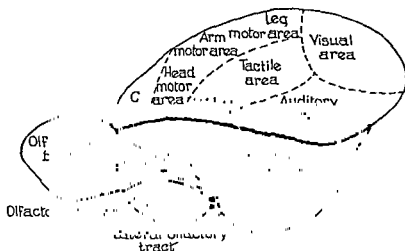


FIG. 207.—LATERAL VIEW OF BRAIN OF MARSUPIAL, SHOWING AREAS OF CORTEX.

Redrawn from G. Elliot Smith.

(Figs 207, 208, 213 and 214). Gennari noted a broad band of white between two layers of gray in the occipital lobe. This band is known as the *stripe of Gennari* (Fig. 209) and is characteristic of the striate area of the occipital lobe. In other parts of the cortex, Baillarger described two thinner bands of white alternating with gray matter. The white bands are called the *inner* and *outer stripes of Baillarger*. The stripe of Gennari is formed by the thickening of the outer stripe of Baillarger.

Elliot Smith has distinguished 28 areas by examination of the fresh or formalin fixed cerebral cortex. Others have shown by histological methods that there are variations: (1) in thickness of the gray matter; (2) in the number, thickness and distinctions of the stripes; (3) in the relative number of myeli-

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is regarded as an olfactosomatic correlation center. Its development is in proportion to the development of the olfactory system in any form. In man with reduced olfactory apparatus it is relatively small.

The NEOCORTEX develops between the archicortex and the paleocortex, pushing

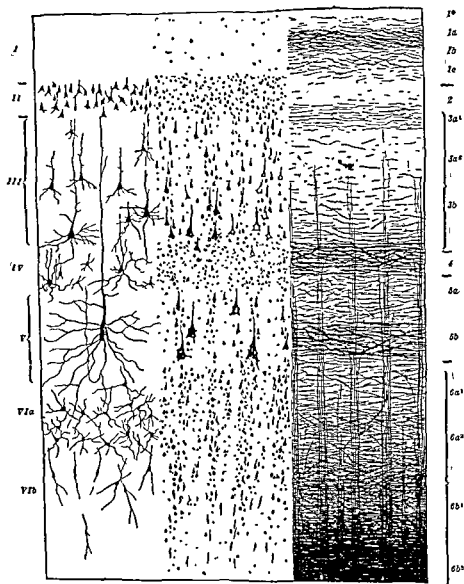


FIG 210—DIAGRAM OF STRUCTURE OF CEREBRAL CORTEX AS SHOWN BY THE GOLGI, THE NISSL AND THE WEIGERT METHODS OF STAINING

From Herrick, *Introduction to Neurology*, W. B. Saunders Co, Philadelphia, 1931.

the archicortex medially and the paleocortex ventrally. The archicortex is rolled into the horn of Ammon and the dentate gyrus around the hippocampal fissure. The paleocortex pushes medially over the olfactory tubercle and forms the endorhinal sulcus.

The neocortex is the general nonolfactory cortex which in man constitutes

tory and other special sensory areas. The *intermediate areas* lie, as a rule, adjacent to the receptive, forming the visuopsychic, the auditopsychic, etc. The *terminal areas* lie between the intermediate zones and together with the intermediate zones occupy the greater part of the surface of the human brain, but a much lesser part of the cortex of lower mammals, with the exception of the anthropoid apes.

In considering the cerebral cortex, distinction must be made between *archicortex*, *paleocortex* and *neocortex*. The archicortex or archipallium is present in amphibians as the medial part of the olfactory area. In man it is made up of the cortex of the *hippocampus*, *dentate fascia* and part of the *hippocampal gyrus*. The dentate fascia receives tertiary olfactory fibers and some visceral fibers from the diencephalon. It is a region of correlation. It shows three layers, namely: (1) a *molecular layer*, consisting of interlacing processes of granule cells and of cells with short processes; (2) a *granule layer*, consisting of ovoid,

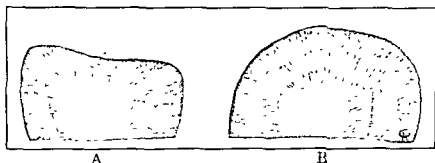


FIG. 209.—SECTIONED SURFACES OF GYRI SHOWING GRAY AND WHITE BANDS OF THE CEREBRAL CORTEX.

A, stripe of Gennari in striate area of occipital lobe. *B*, stripes of Baillarger in cortex of parietal lobe. Magnified $\times 2\frac{1}{2}$.

spherical or pyramidal cells whose dendrites pass to the molecular layer and whose axons pass to the pyramidal cells of the hippocampus and horn of Ammon; (3) a *polymorph layer*, consisting of cells of various forms and sizes, whose axons ascend, in part, to the molecular layer, and in part, descend to the alveus.

The PALEOCORTEX includes the pallial centers of the olfactory tracts. In amphibians it is the lateral part of the olfactory area. In man it includes the uncus and part of the hippocampal gyrus, which together constitute the pyriform lobe. The pyriform lobe (Fig. 207) is sharply marked off from the rest of the cortex by the rhinal fissure and the lateral olfactory tract. In man, due to the modifications of brain surface incident to the development of the temporal lobe and the formation of the insula, the pyriform lobe is connected with the anterior olfactory area by the lateral olfactory tract. In many mammals there is a direct cellular continuity with the anterior olfactory nucleus. The paleocortex is transitional in position and fiber connections between the archicortex and the neocortex. It

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IV. *Lamina granularis interna*, made up of small stellate cells and the outer stripe of Baillarger.

V. *Lamina ganglionaris*, made up of large cells and, in most areas, the inner stripe of Baillarger. In the precentral gyrus this layer contains the giant pyramidal cells of Betz, whose axons form the corticospinal tracts.

VI. *Lamina multiformis*, made up of polymorphic cells.

Kappers makes three groups of the five cellular layers. He combines layers II and III of Brodmann into the *supragranular layers*. Layer IV he calls the granu-

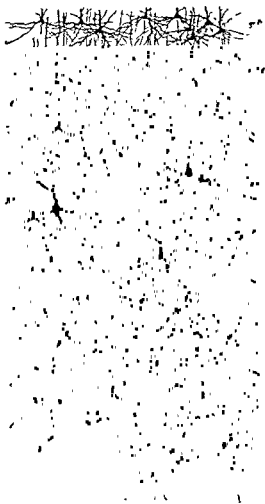


FIG 212—CELLS OF CORTEX OF HUMAN CENTRAL GYRUS GOLGI METHOD. (From Koelliker.)

gr. P., first layer of large pyramidal cells; *kl. P II*, second layer of small pyramidal cells; *PZ*, layer of polymorphic cells; *RP*, giant pyramidal cells.

lar layer, and layers V and VI constitute the *subgranular layers*. The granular layer (IV) of the neocortex is homologous with the granular layer of archicortex and paleocortex. The subgranular layers (V and VI) are homologous with the subgranular pyramidal cells of the older parts of the cortex, but the supragranular pyramids are found in the neocortex only.

The granular layer, according to Kappers, receives and correlates stimuli. The

by far the greater part of the gray matter. It receives somatic impulses from a variety of sources. In most parts of the neocortex five to eight layers are recognizable. Brodmann (Fig. 210) names six fundamental layers as follows, beginning at the surface.

I. *Lamina zonalis* or plexiform layer, made up of nerve fibers tangential to the surface.

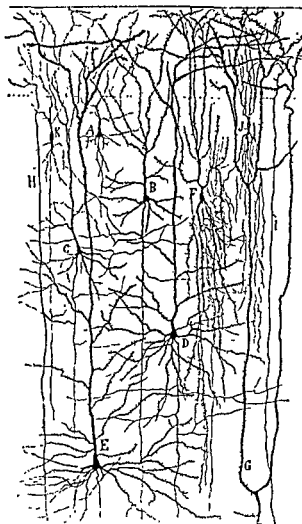


FIG 211—CELLS OF FIRST, SECOND AND THIRD LAYERS OF THE ASCENDING FRONTAL CONVOLUTION OF THE CEREBRUM OF AN INFANT. GOLGI METHOD. (From Cajal)

A, B, C, small pyramidal cells; D, E, medium pyramidal cells; F, cell with dendrites from each end, with axon in the form of a pericellular nest; G, large dendritic process from a large pyramidal cell in the fourth layer; H, I, dendritic processes from cells of fifth and sixth layers; J, small cells with dendrites at each end; K, fusiform cell with long axon.

II. *Lamina granularis externa* or layer of small pyramidal or stellate cells.

III. *Lamina pyramidalis* or layer of medium and large pyramidal cells.

perimental methods have made it clear that some of these regions have special functional significance.

Brodmann makes nine general regions of the neocortex, subdivided into nearly fifty secondary areas. The *general regions* are. (1) *Retrosplenial*, for correlation of olfactory with nonolfactory impulses. (2) *Cingular* (Fig. 218), the



FIG 214.—AREAS OF CEREBRAL CORTEX ACCORDING TO BRODMANN. LATERAL VIEW.

From Herrick, *Introduction to Neurology*, W. B. Saunders Co, Philadelphia, 1937.
(After Brodmann)

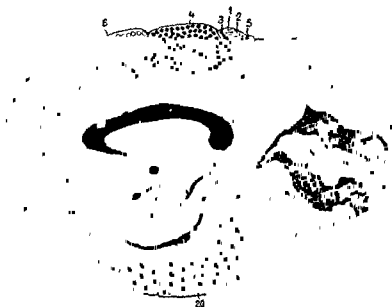


FIG 215.—MEDIAL VIEW OF BRAIN, SHOWING AREAS OF CEREBRAL CORTEX.

From Herrick, *Introduction to Neurology*, W. B. Saunders Co, Philadelphia, 1937.
(After Brodmann)

pyramidal cells of the subgranular layer give rise to efferent axons which carry impulses away from the cortex or form commissural fibers. The supragranular layers also receive and correlate stimuli but the correlative or associative function is predominant. They receive terminal fibers of the corpus callosum and are also the last to develop in the fetus.

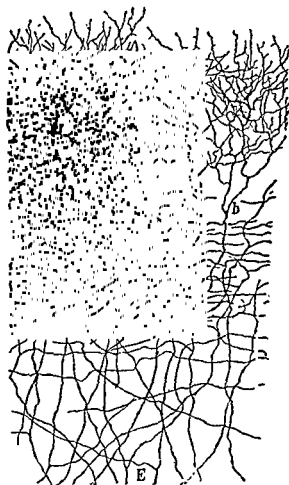


FIG. 213.—SECTION OF HUMAN CEREBRAL CORTEX FROM PRECENTRAL GYRUS, SHOWING FREE ENDINGS OF ENTERING FIBERS.

A, terminal branches near surface; *B*, dense entanglement of terminal arborizations around cell bodies of pyramidal cells of the third layer; *C*, *D*, *E*, horizontally directed nerve fibers giving rise to terminal branches *a*, *b*, in upper part of figure. After Cajal From Herrick, *Introduction to Neurology*, W. B. Saunders Co, Philadelphia, 1931.

The study of variations in the cell layers (cytoarchitectonics) and of variations in arrangement of myelinated fibers (myeloarchitectonics) have made possible histological differentiation of a number of distinct regions in the cortex. Campbell (1905), Brodmann (1909), the Vogts (1926) and others have produced a large literature, both comparative and on human material, in this field. For details reference must be made to the monographs and special articles. Ex-

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absent. The granule cells of the outer and inner granular layers disappear and pyramidal cells are the characteristic cell types. In part of the precentral region (area 4 of Brodmann) the pyramidal cells are of large size, forming the Betz cells located in layer V, which give rise to corticospinal fibers. The frontal part of the precentral region, known as the frontal agranular area (area 6 of Brodmann), has smaller pyramidal cells.

The largest Betz cells lie in the dorsalmost part of the precentral gyrus, near the sagittal fissure. These give off fibers to the muscles of the lower extremity. The muscles of the lower part of the body have their innervation from the

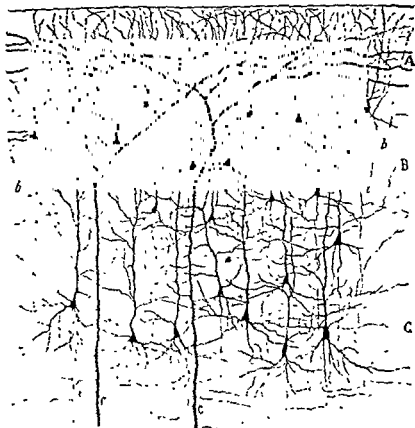


FIG. 217.—CELL TYPES IN SUPERFICIAL PART OF VISUAL CORTEX OF INFANT.
GOLGI METHOD (From Cajal)

A, plexiform layer; *B*, layer of small pyramidal cells; *C*, outer part of layer of large and medium pyramidal cells, *a*, axon; *b*, collateral; *c*, dendritic process.

more dorsal parts of the motor area, the upper parts of the body from the middle region of the precentral gyrus, while the facial muscles, tongue, pharynx, etc., are represented in the ventralmost part of the gyrus.

The *postcentral region* (Fig. 221) is thinner and has a well marked inner granular layer (IV) and the typical six layers. The pyramidal cells of layer V are smaller and less numerous than in the precentral region. The supragranular pyramidal layer (III) is well developed. This region is of sensory type.

The *temporal region* (Figs. 216 and 222), part of which is auditory in function, has a well developed internal granular layer (IV), especially in the trans-

supracallosal part of the limbic lobe, having to do with olfactory sense. (3) *Precentral* (Fig. 219), chiefly motor. (4) *Frontal granular* (Fig. 220), the frontal association center. (5) *Postcentral*, tactile. (6) *Parietal*, sensory and parietal

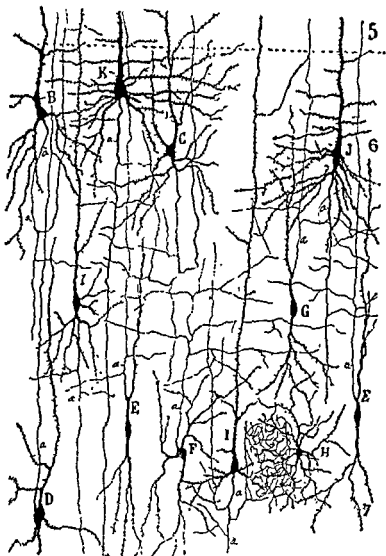


FIG 216.—CELL TYPES IN 6TH LAYER OF TEMPORAL CORTEX OF INFANT. GOLGI METHOD.

5, layer of granules; 6, deep layer of medium size pyramidal cells; B, D, large cells with long ascending axons, C, large cell with long axon and ascending collaterals; E, G, small cells with ascending axons, F, cell with short branching axon; H, neuroglia like cell; I, small fusiform or pyramidal cells; J, K, large pyramidal cells with long axons; a, axon (From Cajal.)

association centers. (7) *Temporal*, partly auditory (Fig. 216). (8) *Insular*, function unknown (9) *Occipital*, visual, in part (Fig. 217).

Only a few of the best known regions will be compared briefly, to illustrate the structural and functional differences.

The *precentral region* (Figs. 213 and 219) includes the thickest part of the cerebral cortex, part of it attaining a depth of 4 mm. The stripes of Baillarger are

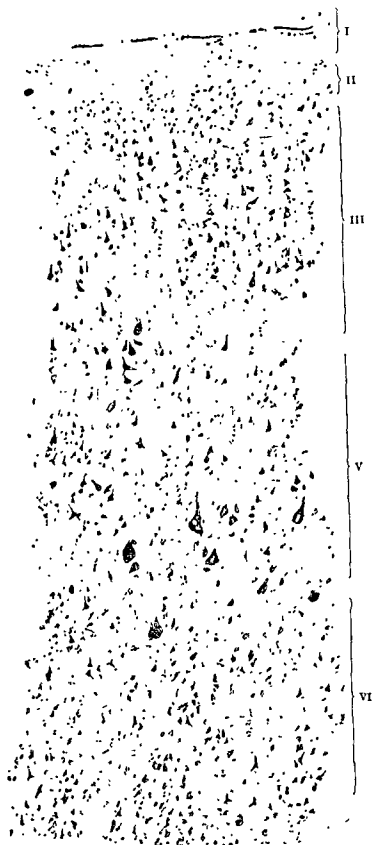


FIG 219—CELL LAYER IN THE PRECENTRAL REGION.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co., New York, 1936

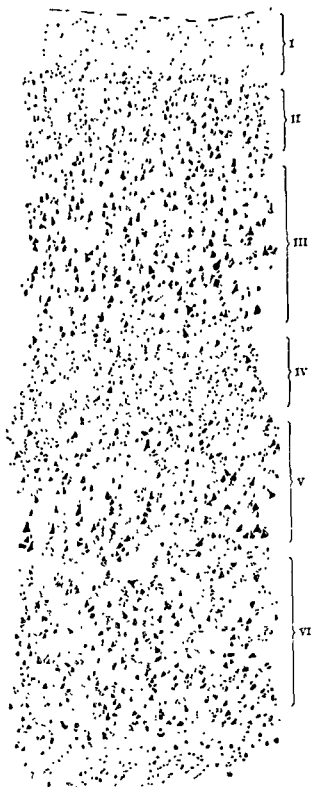


FIG. 218—CELL LAYERS IN CINGULUM.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co, New York, 1936.

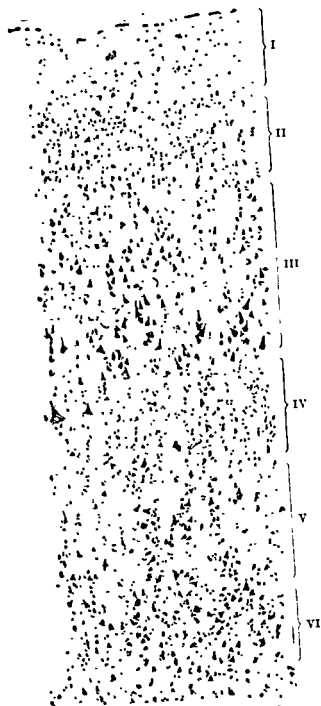


FIG. 221.—CELL LAYERS IN THE POSTCENTRAL REGION.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co., New York, 1936

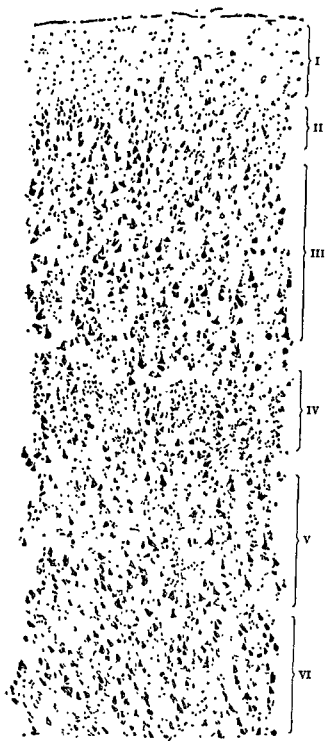


FIG. 220—CELL LAYERS IN THE FRONTAL GRANULAR REGION.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co, New York, 1936

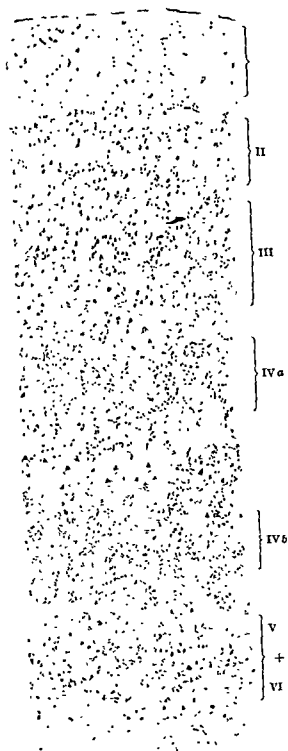


FIG 223.—CELL LAYERS IN THE OCCIPITAL REGION.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co, New York, 1936.

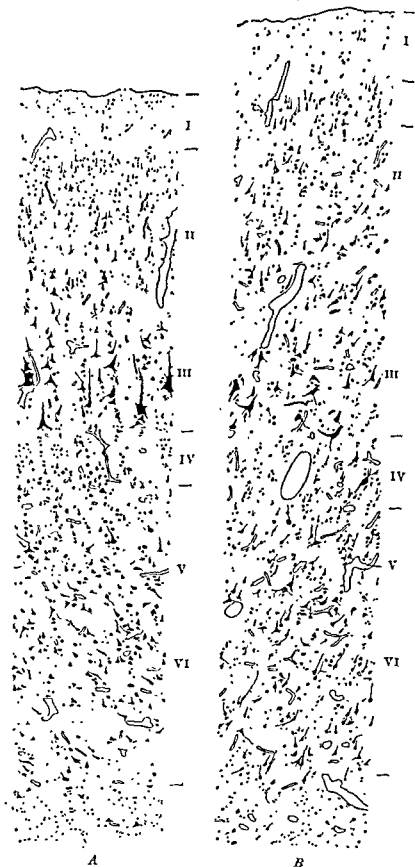


FIG. 222—CELL LAYERS IN THE TEMPORAL REGION.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co, New York, 1936.

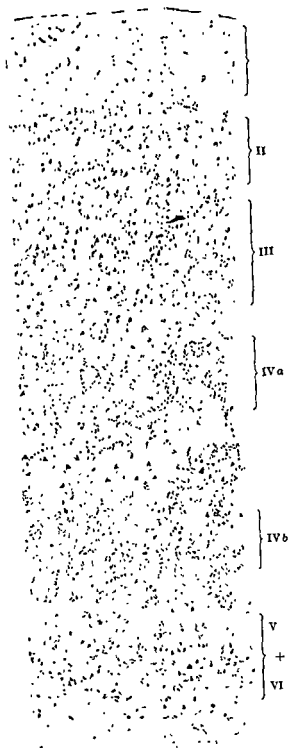


FIG 223—CELL LAYERS IN THE OCCIPITAL REGION.

From Kappers, Huber and Crosby, *Comparative Anatomy of the Nervous System*, The Macmillan Co, New York, 1936.

verse temporal gyrus. The deeper layers V and VI are not well differentiated, but the pyramidal layer (III) has large pyramidal cells.

The *occipital region* (Figs. 217 and 223), although its cortex as a whole is thin, shows a great thickening of the deep granular layer (IV). In the striate area, due to the entrance of the optic radiations, this doubles in thickness but

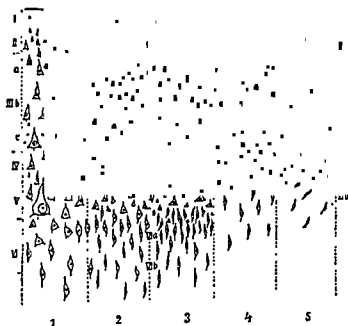


FIG. 224.—DIAGRAM OF THE FIVE STRUCTURAL TYPES OF CEREBRAL CORTEX, ACCORDING TO CYTO-ARCHITECTURAL PATTERNS. (From Cajal.)

returns to ordinary thickness in the regions surrounding the striate area. The supragranular pyramidal layer (III) has large pyramidal cells, as does the ganglionic layer (V). The striate area receives the visual projection fibers and is the center for conscious vision. The surrounding parts of the occipital cortex are regarded as visual association areas.

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CHAPTER 23

THE EFFERENT SYSTEMS

The efferent or motor systems have been considered in part in connection with various divisions of the nervous system so far described. In the present chapter they will be considered as units.

THE VOLUNTARY MOTOR SYSTEM.—The chief tracts of the strictly volitional motor system are the lateral and ventral corticospinal or pyramidal tracts and the corticobulbar tract. They have their origin from cells of layer V in the precentral gyrus of the cerebral cortex (area 4 of Brodmann). The fibers are usually described as axons of the Betz cells, some of which are among the largest nerve cells in the body. However, there are about three times as many fibers in the pyramidal tract as it emerges from the brain as there are large pyramidal (Betz) cells in the precentral gyrus. Some of the fibers must have their origin in smaller pyramidal cells.

The *precentral gyrus* has been shown to have a definite pattern of localization of cells whose fibers pass to specific groups of muscles. The lower portions of the body are supplied from the upper parts of the motor field, and the upper body parts from the lower part of this field. Thus the muscles of the toes and foot have the cells of their upper motor neurons adjacent to the sagittal fissure, while the muscles of the face, tongue, palate and larynx have their upper motor neuron cells in the part of the gyrus near the fissure of Sylvius. The various other regions of the body are supplied from appropriately placed intermediate zones

The motor fibers descend from the cortex into the internal capsule. Here the corticobulbar fibers form two bundles at the genu, while the corticospinal fibers have their position in the posterior limb. Those to the upper part of the body lie in the forward part of the posterior limb, while those to the lower trunk and leg lie in the middle zone.

From the internal capsule the fibers continue into the basis pedunculí. Here again they assume specific positions. The corticospinal bundles occupy the middle three-fifths of the peduncle. The corticobulbar fibers form two bundles, the *medial* tract at the medial border of the base of the peduncle, and the *lateral* between the lateralmost part of the corticospinal bundle and the substantia nigra. They continue through the basilar region of the pons, forming large bundles separated by transverse pontile fibers.

The *corticobulbar tract* (Fig. 225) including fibers to the IIIrd and IVth motor nuclei of the midbrain, begins to separate from the internal capsule

verse temporal gyrus. The deeper layers V and VI are not well differentiated, but the pyramidal layer (III) has large pyramidal cells.

The *occipital region* (Figs. 217 and 223), although its cortex as a whole is thin, shows a great thickening of the deep granular layer (IV). In the striate area, due to the entrance of the optic radiations, this doubles in thickness but

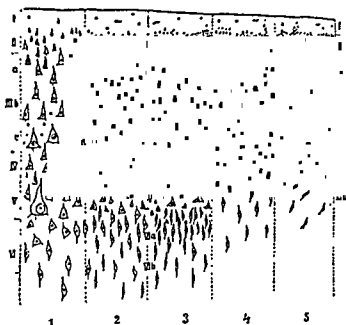


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at the upper end of the midbrain. Bundles of fibers called by Dejerine *aberrant pyramidal fibers* of the peduncle enter the reticular formation and pass to the eye muscle nuclei of the midbrain. Aberrant fibers of the pons and of the bulb are also recognized as small bundles with much variation. The aberrant bundles of pons and medulla oblongata end in relation to the motor Vth, the VIth, the VIIth, XIth and XIIth nuclei and the nucleus ambiguus supplying the voluntary muscles of the face and head. Some of these fibers reach the upper part of the cervical spinal cord. The corticobulbar fibers decussate in part at the level of the nuclei they supply. They form small bundles to each of the somatic motor nuclei of the medulla oblongata and to the upper segments of the spinal cord.

On emerging from the pons the main mass of fibers continues as the pyramids of the medulla oblongata. Most of the fibers cross at the decussation of the pyramids to form the greater part of the lateral corticospinal or pyramidal tract. Others pass into this tract without crossing. Still others continue directly from the pyramids into the ventral funiculus of the cord as the ventral corticospinal or pyramidal tract. The latter is usually stated to extend only into the cervical or upper thoracic part of the spinal cord, but Erb has shown that it may reach the sacral region. The uncrossed pyramidal fibers are usually said to decussate within the cord in their segments of termination. Many, however, end on the side of origin.

The Lower Motor Neuron—The pyramidal tract fibers terminate in synaptic relation to large motor cells in the anterior column of the gray matter of the spinal cord. Recent studies indicate that the majority of fibers (80 to 90 per cent in chimpanzees and monkeys) end on intermediate neurons, while 20 to 25 per cent form connections on the side of origin of the fibers. The lower motor neuron cells outnumber the corticospinal fibers, so that each of the latter appears to have synaptic connections with several motor cells. The axons of the latter form the anterior motor roots of the spinal nerves.

EXTRAPYRAMIDAL MOTOR PATHS (Fig. 226).—Fibers from other parts of the cerebral cortex than area 4 of Brodmann also have a part in movements of the voluntary muscles. Stimulation of certain parts of area 6 of the frontal lobe, area 5 of the parietal lobe, area 22 of the temporal lobe, etc., after destruction of area 4, produce complex movements of trunk and extremities, head and eyes. The impulses, instead of passing through direct fibers to the anterior column of the spinal cord, are relayed through a pathway of several links, including the striate body, the substantia nigra and the tegmental region of the midbrain.

The *premotor area* (area 6) is the best known, experimentally and clinically, of the extrapyramidal regions named. It lies immediately in front of motor area 4, and in part, is included in the precentral gyrus. When area 4 is destroyed or the pyramidal tract is interrupted, stimulation of the premotor area produces muscular responses in the form of mass movements of the opposite half

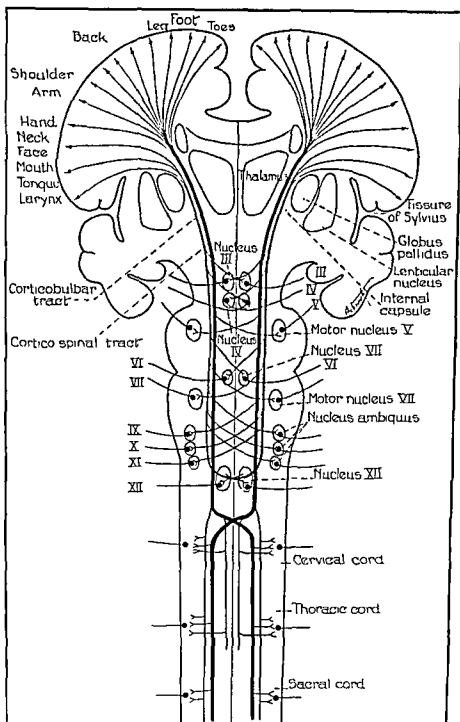


FIG. 225—THE CORTICOSPINAL AND CORTICOBULBAR PATHS (PYRAMIDAL SYSTEM)

THE EFFERENT SYSTEMS

segments of the extremities, such as of individual fingers, however, are no longer possible.

After injury to the pyramidal system compensation is established in time, apparently through coöperative action of the extrapyramidal motor areas of the affected hemisphere and the appropriate region (e.g., leg area) of the motor cortex of the other hemisphere. The possibility of innervating single muscle groups is restored. The stereotyped extrapyramidal synergies may be modified by pyramidal tract influences from the unaffected side. Compensation, however, is never complete (Foerster).

In addition to stereotyped movements of the kind described, the extrapyramidal system also serves associated movements, such as swinging of the arms in walking, movements of postural changes, etc. Isolated movements of single segments, on the other hand, are represented only in motor area 4 of the cortex. Therefore individual movements of fingers or toes, hand or foot, arm or leg, thigh, etc., are lost if the arm or leg areas of the motor cortex, or the pyramidal tract fibers coming from them, are destroyed.

The extrapyramidal system is more primitive and of earlier phylogenetic development than the pyramidal. It has to do with mass movements and synergic movements of groups of muscles, while the specific function of area 4 of the pyramidal system "is the isolated innervation of single muscle groups" (Foerster). The extrapyramidal system may be considered as *paleokinetic*, while the pyramidal system is *neokinetic*.

The Corticopontocerebellar Path.—Axons from pyramidal cells of the frontal lobe (area 10 of Brodmann) and of the temporal lobe form the *frontopontine* and *temporopontine tracts*, respectively. The frontopontine fibers pass through the anterior limb of the internal capsule and the medial fifth of the basis pedunculi, to enter the pons. They end in the pontine nuclei. The temporopontine fibers pass through the tip of the posterior limb of the internal capsule and through the lateralmost part of the basis pedunculi. They end in the more dorsal pontine nuclei. Collaterals from the pyramidal tracts also end in the pontine nuclei. The nuclei of the pons give rise to the great mass of fibers which constitute the pons. The fibers decussate and enter the cortex of the opposite hemisphere of the cerebellum through the brachium pontis.

Cerebellorubral and Cerebellothalamic tracts—The dentate nucleus of the cerebellum gives rise to the brachium conjunctivum. This ends in part in the red nucleus and in part in the thalamus. The *cerebellorubral* fibers make connections with the rubrospinal tract, forming a cerebellorubrospinal pathway. The cerebellothalamic impulses are relayed to the frontal cortex and influence its motor activity. Through connections between thalamus and the striate body these impulses probably affect the extrapyramidal system also.

of the body. Isolated muscular movements are lost. The experimental studies of *Fulton on primates* and the clinical studies of *Foerster* have made clear the general functions of this system.

The details of the pathway involved are not firmly established, but fibers from the motor and premotor areas terminate in the caudate nucleus, the globus pallidus, the red nucleus, the tegmental region of the mid-brain and the substantia nigra (Poljak, 1932). From the striate body, especially from the globus pallidus, the ansa lenticularis carries impulses to the tegmental nuclei and substantia nigra. In these centers the relayed impulses, together with impulses reaching

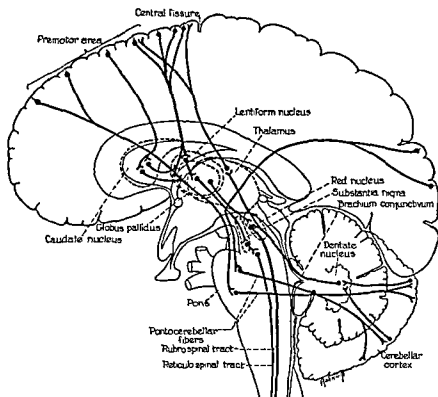


FIG. 226.—EXTRAPYRAMIDAL SYSTEMS, CORTICO-STRIO-SPINAL AND CORTICO-PONTO-SPINAL SYSTEMS

these nuclei directly from the cortex, are integrated and relayed to the spinal cord. The paths involved are the rubrospinal, possibly the reticulospinal tracts, and the medial longitudinal bundle.

Muscular actions produced by stimulation of the extrapyramidal areas are compound movements of all the segments of the arm or leg and stereotyped movements of groups of muscles (synergies) such as the extensor synergy or the flexor synergy. When normal voluntary movements are performed the pyramidal and extrapyramidal systems cooperate. If the pyramidal path is interrupted, voluntary movement is not entirely lost. Isolated movements of single

segments of the extremities, such as of individual fingers, however, are no longer possible.

After injury to the pyramidal system compensation is established in time, apparently through coöperative action of the extrapyramidal motor areas of the affected hemisphere and the appropriate region (e.g., leg area) of the motor cortex of the other hemisphere. The possibility of innervating single muscle groups is restored. The stereotyped extrapyramidal synergies may be modified by pyramidal tract influences from the unaffected side. Compensation, however, is never complete (Foerster).

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CHAPTER 24

FUNCTIONS OF THE THALAMUS AND THE CEREBRAL CORTEX

The nervous system has many gateways that open inward, admitting stimuli of diverse sorts from the skin, muscles, joints, viscera and special sense organs. Within the brain and spinal cord there are several levels of functional activity, from simple reflexes to highly integrated responses. Reflexes are simple forms of behavior which conform to a fixed pattern determined by the receptors and effectors concerned. In integration there are brought about various combinations of nervous activities and reflexes in such a way that they cooperate in a larger activity to unify the functions of the body as a whole. At the lowest level of nervous activity involving the central nervous system is found the simple reflex arc, including only a receptor, a simple correlation center and an effector of one segment of the body. Somewhat more complex may be the reflex arc extending to other segments of the spinal cord which may involve responses by the motor apparatus of several segments.

The various functional types of primary afferent neurons, in addition to forming reflex arcs, as described in previous chapters, also make connections in the cord which bring about grouping of fibers into functional tracts. In these all the sensations of the same type, as pain, touch, temperature, etc., ascend together. Furthermore, the afferent stimuli which may affect consciousness, i.e., the sensory stimuli, are segregated in the cord from the nonsensory impulses which are concerned with the more elaborate reflex systems served by the brain stem and the cerebellum.

THALAMUS

The sensory impulses reach the thalamus, the nonsensory reach the cerebellum and the reflex centers of the brain stem. Thus the spinal cord, in addition to its reflex function, transforms impulses from the first sensory or reflex level to the secondary sensory level served by the thalamus. The nerve fibers from spinal cord to thalamus belong to neurons of the second order. Likewise the nonsensory afferent impulses destined for the more elaborate reflex activities of muscular coordination, etc., are segregated in the spinal cord and relayed through neurons of the second order to higher brain centers. Within the thalamus the different functional types of impulses are distributed to the various nuclei. As described

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pulses so that pain and reactions to it, which are responses for body protection, do not become predominant in our activities. According to Drinker the severity of pain is ordinarily lessened by inhibition from the cortex. This allows discrimination as to the source, seriousness, and possible means of avoidance or cessation of the stimulus. "If pain were too violent we should be reflexly withdrawing, running or snarling on all occasions."

In addition to pain and temperature impulses, the thalamus receives impulses of touch, pressure, and conscious proprioceptive impulses, as well as integrated proprioceptive impulses from the cerebellum which do not reach consciousness. As already stated, there are also the special sensory impulses to the geniculate bodies. Impulses of visceral sensibility are regarded as reaching the thalamus, since visceral stimuli produce greater discomfort as well as more marked response in "thalamic" cases. Pleasurable visceral stimuli are also increased.

In general the thalamus may be considered as a relay station for all sensory impulses into other areas of the thalamus or into the cerebral cortex. In the thalamus certain sensations are consciously recognized, particularly those of pleasure and pain, comfort and discomfort, and probably emotion. These, however, are of the "all or nothing" type. The threshold of stimulus is raised but the effect is also increased out of proportion to the stimulus. Patients with lesions of the cortex on one side, involving loss of cortical recognition of stimuli, state that thermal stimuli are hotter or colder on the affected side, where they reach only the thalamus, than they are on the normal side. Other stimuli produce greater discomfort or greater pleasure sensation on the affected side, if felt at all, than on the normal side. For impulses involving awareness and primitive protective reactions beyond the spinal reflex level the thalamus may be regarded as an end organ. The impulses may be relayed to the cerebral cortex for finer discrimination. Thalamic function is concerned with the quality of sensations, while cortical function has to do with discrimination.

THALAMIC SYNDROME (SYNDROME OF DEJERINE-ROUSSY).—This syndrome shows many variations, according to the location and size of the lesion. It is characterized by diminished sensation in the entire half of the body opposite the lesion, deep pressure, point discrimination, sense of position, etc., being more markedly affected than pain, temperature or light touch sensibility. There are severe spontaneous paroxysms of uncontrollable pain and exaggerated responses to pain and temperature stimuli when these pass the heightened threshold of receptivity. Some motor paralysis, diminished muscle tone, muscular incoordination, tremor and involuntary spasmodic movements also may appear on the side opposite the lesion. The sensory and motor disturbances are due to involvement of the respective pathways or of their way stations in or near the thalamus. The ataxia, diminished tone and spasmodic, choreiform movements are regarded as due to involvement of the cerebellar pathway to the cerebral cortex.

in Chapter 17 the thalamus consists of a number of nuclei receiving groups of secondary fibers and projecting fibers of the third order to the cerebral cortex. The posteroventral nucleus receives exteroceptive and proprioceptive stimuli from the spinal cord and the trigeminal nuclei of the medulla oblongata. It projects fibers to the postcentral convolution of the cortex (areas 3-1). The lateroventral nucleus receives integrated nonsensory impulses from the cerebellum and projects fibers to the precentral and premotor areas of the cortex (areas 4 and 6 of Brodmann).

The posteromedial ventral nucleus receives secondary fibers from the face and neck and projects to the sensory face area in the postcentral convolution (areas 3-1 of Brodmann). The posterolateral ventral nucleus receives secondary exteroceptive fibers from the arm, trunk and leg and projects to the sensory arm, trunk and leg areas of the postcentral gyrus (areas 3-1 of Brodmann).

Other parts of the thalamus, as described in earlier chapters, receive and project special somatic sensory fibers. The lateral geniculate body receives the optic fibers, which are neurons of the second order, from the retina, and projects neurons of the third order to the visual cortex of the occipital lobe (area 17). The medial geniculate body receives fibers from the auditory centers of the medulla oblongata and projects to the transverse temporal gyri of the temporal lobe (areas 41 and 42). The olfactory fibers also are projected from olfactory centers such as the amygdaloid nucleus, which are nonthalamic, to the uncus and uncinate gyrus of the archicortex. These projection fibers to distinct areas of the cerebral cortex carry only their respective types of stimuli. The cortical areas involved receive these as their principal and characteristic afferent impulses.

Many of the stimuli received by the skin and sense organs never reach the cortex. The thalamus exerts a selective inhibition which may be illustrated as follows (Evans): If the "cold spots" on the hand, after being localized by a blunt rod cooled, for example, to 15° C., are stimulated by a rod heated to 45° C., the sensation experienced is still that of cold. If instead of a rod a larger surface capable of stimulating a considerable skin area, including both "warm" and "cold" spots, be applied to the skin after being heated to 45° C., the sensation is one of warmth only. The response of the "cold" spots fails to reach consciousness. This selection must take place in the thalamus, illustrating an important function of this part of the brain as the antechamber to the cerebral cortex.

Not all stimuli need be relayed to the cortex to be felt. Impulses of pain, pressure, heat or cold appear to be recognized in the thalamus. This has been shown by responses of animals from which the cortex has been removed, as well as in human cases with complete destruction of the sensory cortex. Judgment of intensity of the stimulus, localization, etc., however, are lost. Head holds that the thalamus is the terminal organ of the nervous system for pain and temperature sensations but that it is under the dominance of the cerebral cortex. There is evidence that the cortex inhibits overactivity of sensory im-

pulses so that pain and reactions to it, which are responses for body protection, do not become predominant in our activities. According to Drinker the severity of pain is ordinarily lessened by inhibition from the cortex. This allows discrimination as to the source, seriousness, and possible means of avoidance or cessation of the stimulus. "If pain were too violent we should be reflexly withdrawing, running or snarling on all occasions."

In addition to pain and temperature impulses, the thalamus receives impulses of touch, pressure, and conscious proprioceptive impulses, as well as integrated proprioceptive impulses from the cerebellum which do not reach consciousness. As already stated, there are also the special sensory impulses to the geniculate bodies. Impulses of visceral sensibility are regarded as reaching the thalamus, since visceral stimuli produce greater discomfort as well as more marked response in "thalamic" cases. Pleasurable visceral stimuli are also increased.

In general the thalamus may be considered as a relay station for all sensory impulses into other areas of the thalamus or into the cerebral cortex. In the thalamus certain sensations are consciously recognized, particularly those of pleasure and pain, comfort and discomfort, and probably emotion. These, however, are of the "all or nothing" type. The threshold of stimulus is raised but the effect is also increased out of proportion to the stimulus. Patients with lesions of the cortex on one side, involving loss of cortical recognition of stimuli, state that thermal stimuli are hotter or colder on the affected side, where they reach only the thalamus, than they are on the normal side. Other stimuli produce greater discomfort or greater pleasure sensation on the affected side, if felt at all, than on the normal side. For impulses involving awareness and primitive protective reactions beyond the spinal reflex level the thalamus may be regarded as an end organ. The impulses may be relayed to the cerebral cortex for finer discrimination. Thalamic function is concerned with the quality of sensations, while cortical function has to do with discrimination.

THALAMIC SYNDROME (SYNDROME OF DEJERINE-ROUSSY).—This syndrome shows many variations, according to the location and size of the lesion. It is characterized by diminished sensation in the entire half of the body opposite the lesion, deep pressure, point discrimination, sense of position, etc., being more markedly affected than pain, temperature or light touch sensibility. There are severe spontaneous paroxysms of uncontrollable pain and exaggerated responses to pain and temperature stimuli when these pass the heightened threshold of receptivity. Some motor paralysis, diminished muscle tone, muscular incoördination, tremor and involuntary spasmodic movements also may appear on the side opposite the lesion. The sensory and motor disturbances are due to involvement of the respective pathways or of their way stations in or near the thalamus. The ataxia, diminished tone and spasmodic, choreiform movements are regarded as due to involvement of the cerebellar pathway to the cerebral cortex.

GENERAL CONSIDERATIONS ON CORTICAL FUNCTION

Since, in other organs of the body, structural specialization means functional difference, it is held by many that such is more or less the case in the histologically different parts of the cerebral cortex generally. The phylogenetic development of various parts of the brain, as shown by comparative neurologists, indicates that specialization of function goes hand in hand with specialization of brain structure. Certain parts of the cortex clearly show this in man as already noted. The striate area of the occipital lobe, for example, is obviously a localized part of the cerebral cortex for reception of conscious visual stimuli. There is even a very definite projection upon it from specific parts of the lateral geniculate body, which in turn has specific regions for termination of fibers from

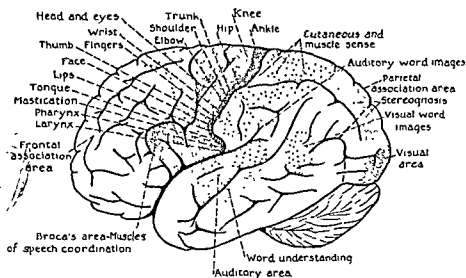


FIG 227.—LATERAL VIEW OF LEFT CEREBRAL HEMISPHERE SHOWING AREAS OF FUNCTIONAL LOCALIZATION

definite quadrants and zones of the retina. Also the motor area (area 4) shows an increase of size of the pyramidal cells in layer V, together with reduction of the granular layers, giving it differentiation of structure. These are examples of *projection areas*, the one sensory, the other motor, which have definite patterns of structure associated with specific functional type. The other chief ascending projection systems also terminate in specific and more or less clearly defined cortical areas.

A second type of functional localization is shown by the *association systems* between different parts of the brain. The cells and fibers of these systems have a fixed pattern of arrangement and are regarded as forming the anatomical basis for segregating the sensory experiences produced by the various stimuli which reach the analytic sensory projection areas. In the *association areas* these different experiences are believed to be recombined into various patterns of response

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(Herrick). These patterns are then carried to performance through the motor projection areas.

The cerebral cortex is thus made up of *projection areas* and *association areas*. The latter are the most significant features of the brain in man. Associational fibers are found in all parts of the cortex. Associational areas and projection areas are not sharply separated, for projection fibers, while more concentrated in the specific projection areas, are found also in the association areas, especially in the zones immediately adjacent to the projection areas. The various parts of the brain are so interconnected by associational pathways that normally the entire organ must be regarded as functioning as a unit. Some local areas, however, may be brought to specific functional activity by local stimulation or by local application of strychnine. Severe injury to one part, on the other hand, may throw the whole organ out of orderly functional activity for a time, as in the

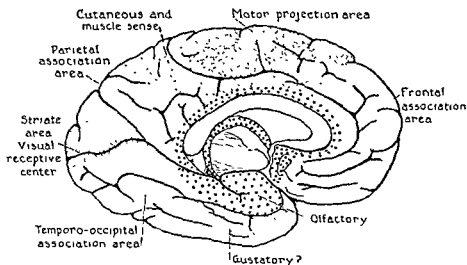


FIG 228—MEDIAL VIEW OF LEFT CEREBRAL HEMISPHERE SHOWING AREAS OF FUNCTIONAL LOCALIZATION.

shock and loss of consciousness of apoplectic stroke. In such cases, however, unless there has been very serious injury to a considerable part of the brain, consciousness returns and most of the nervous functions are gradually restored. The function of destroyed cerebral tissue, however, is not restored.

The association areas are to be regarded as focal points of association tracts and fibers, rather than cortical areas of specific mental functions (Herrick). Such associational foci are regarded as the necessary mechanism for memory, which appears to be a function of the associational cortex. In such areas as the visual-psyche and the auditory-psyche centers, where certain types of function are specifically performed, there is probably a preponderance of specific fiber systems.

A third system of connections in the cortex consists of a mass of unspecialized nervous tissue which infiltrates the association and projection areas. In lower mammals, like the rat, the intermingling of nonspecific tissue with the sensory

and motor projection areas is very considerable. In the higher primates the latter areas have become more and more segregated into structurally specialized and functionally more or less specific areas. The association areas between them have increased in extent. In man the process of specialization of certain regions has gone even further as pointed out above, but a great mass of the generalized type of nervous tissue remains. This permeates throughout the projection and association areas as well as the less specifically organized parts of the cortex. In contrast to the highly organized striate area, for example, which serves only visual function, this nonspecific tissue varies in function from moment to moment and is the plastic material of the cortex.

In the light of these general considerations some of the more important conclusions from experimental and clinical study of cerebral function may be described with greater understanding. Lashley, as the result of training rats in conditioned reflexes and subsequently destroying parts of their brains, concluded that their capacity to learn was reduced in proportion to the amount of brain tissue destroyed, without reference to the patterns of the cyto-architectonic fields removed. In other words, the total volume of cortical tissue, rather than anatomical specialization, appeared to be the determining factor. Destruction of a projection area, such as the visual cortex, in the rat, results in sensory loss for a time, but restoration of function by neighboring parts of the cortex is soon accomplished. In man functional restoration occurs to a limited extent, after destruction of some parts of the brain. This is more marked in the infant than in the adult. Some forms of sensation, however, are permanently lost in man after their areas are destroyed.

Pavlov found that removal of the posterior portions of the cerebral cortex in dogs destroyed the activity of the analyzers for acoustic and visual reflexes, while tactile reflexes were little disturbed. Bilateral removal of the anterior half of the cerebral cortex destroyed the tactile analyzer, but had little effect on visual or auditory conditioned reflexes. Removal of the temporal lobes produced greatest damage to auditory conditioned reflexes, although it did not completely destroy them. The dog could learn to respond to single tone stimuli, but not to complex sounds such as calling his name. Pavlov concluded that the function of the cerebral cortex is to establish new nervous connections and thus to ensure proper functional correlation between organism and environment. It is the essential organ for establishing and maintaining conditioned reflexes.

THE MOTOR CORTEX

Experimental studies on animals, including primates and the more recent studies of Foerster, Penfield and others on man, have demonstrated clearly that area 4, the "strip area" of the precentral gyrus, when stimulated, as by an electric current, gives rise to isolated movements of single muscles or of groups of muscles on the opposite side of the body. The general pattern of localization

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appears to be the same in various mammals. Elliot Smith indicates leg, trunk and arm areas in the marsupial cortex. The number of points giving rise to discrete movements increases in the phylogenetic scale, being more numerous in the higher apes than in monkeys and more numerous in man than in the apes. Penfield also has elicited vocalization in man by stimulating a small part, area 4c, of the motor area. This was done in conscious patients during the surgical removal of brain tumors. The vocalization could not be voluntarily suppressed when elicited by stimulation. Another focus, slightly rostral to area 4c, on stimulation, can inhibit voluntary sound production. Destruction of area 4, on the other hand, results in paralysis of voluntary movements, especially skilled movements. Here again the degree of motor paralysis is greater in man and the higher apes than in the lower forms.

The giant pyramidal cells of Betz, found in layer V of the cortex of area 4, have been proved to be chiefly responsible for individual movements such as described. When these cells are destroyed, stimulation of the area produces no responses. Section of the pyramidal tracts also results in loss of the responses, and in chromatolysis of the Betz cells. Young animals are unable to perform individual movements before the Betz cells and their fibers are completely developed. There is therefore evidence for specific function by at least one individual type of cortical cell. It has long been known that destruction of the motor cortex on one side results in permanent motor paralysis on the opposite side of the body.

The functions of the cerebral cortex have been studied by animal experimentation as well as by clinical observation. Early in the 19th century Gall and Spurzheim established the school of the phrenologists, who held that there are centers in the brain for various mental characteristics. These, it was claimed, could be determined by study of the areas on the skull presumably raised by hypertrophy of the brain parts beneath. The French physiologist, Flourens, showed the falsity of this view and concluded from his experiments on animals that the cortex must function as a whole, with no specific areas. Fritsch and Hitzig, however, in 1870, demonstrated that certain parts of the cortex, on electrical stimulation, produce muscular responses.

Area 4 receives fibers from the postcentral gyrus (areas 3-1-2, especially) in the form of short arcuate fibers. Impulses received by this sensory area are relayed to the motor area through this connection. The postcentral gyrus was, indeed, first thought to be the motor area since muscular response to stimulation behind the central fissure was obtained. Subsequent studies, including section through the cortex between precentral and postcentral gyri, followed by stimulation of area 4 of the precentral gyrus, have localized the motor area as above described. Area 4 also receives projection fibers from the thalamus which relay unconscious proprioceptive impulses from the cerebellum. These undoubtedly play a rôle in governing the initiation of impulses in the motor area.

Other areas of the cortex also are capable of giving rise to muscular move-

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VISCERAL MOTOR FUNCTIONS OF THE CEREBRAL CORTEX

The cerebral cortex exercises a control over visceral functions also. It has long been known that in man the extremities of the affected side show increased temperature in the acute stages of hemiplegia. In old standing cases, however, the temperature is usually lower on the affected than on the normal side. Experimental destruction of area 4 in monkeys was followed by reduced temperature

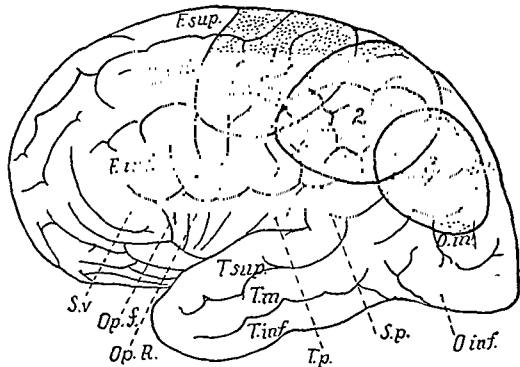


FIG. 230—ZONES OF APRAXIA.

1, zone in which lesions produce inability to carry out purposive voluntary movements (glidekinetic apraxia); 2, zone in which lesions are followed by disturbance of initiation of movement (ideokinetic apraxia); 3, zone in which lesions are followed by loss of memory and idea of acts (ideational apraxia).

Ca., precentral gyrus; Cp., postcentral gyrus; F.inf., inferior frontal gyrus; F.med., medial frontal gyrus; F.sup., superior frontal gyrus; G.sm., supramarginal gyrus; O.inf., inferior occipital gyrus; O.m., medial occipital gyrus; Op.f., frontal operculum; Op.r., operculum; Os., superior occipital gyrus; S.p., posterior limb of Sylvian fissure; S.v., anterior limb of Sylvian fissure; T.inf., inferior temporal gyrus; T.m., medial temporal gyrus; T.p., deep temporal gyrus; T.sup., superior temporal gyrus. From Papez, after P. Bailey, *Arch. Neur. & Psychiat.*, Vol. 11, 1924, copied from Liepmann.

in the opposite extremities (Kennard). Such changes must be due to peripheral vasomotor effects. Electrical stimulation of areas 4 and 6 in animals has resulted in both vasoconstriction and vasodilatation, according to the area stimulated. Cardiovascular effects, including changes in blood pressure and heart rate, as well as effects on the digestive tract, have been produced by electrical stimulation of the cerebral cortex. The production of perspiration is also affected by the cortex, which seems to have a part in the heat regulation of the body. The region from which such effects may be induced are largely intermingled with motor areas 4

cause the parts of the brain included in them do not show the six layers characteristic of the neocortex (isocortex of Vogt). Most of their connections indicate that they are associated with olfactory function. There is some evidence, not conclusive, for adding gustatory and other visceral sensory functions. In mammals which have no olfactory bulb (water mammals like the porpoise) the archicortex is much reduced. Man and primates, with small olfactory bulbs and reduced olfactory sense (microsmatic animals), nevertheless show a very large development of the archicortex. In the opossum, which is one of the most primitive of living mammals, the olfactory centers are greatly developed. The parts of the cerebrum related to smell are the most prominent portions of the cerebral hemispheres, the two sides being connected by the large anterior commissure.

The neocortex of the opossum is relatively simple and has no corpus callosum, such connections as exist between its two sides apparently being served by the anterior commissure. The neocortex in all mammals primitively serves as the projection cortex for general body sense, sight, hearing, and combinations of these. The first part of the neocortex to develop in the rat is the parietal region. This is followed by differentiation of other areas. When it reaches the stage of functional development demanding considerable association between the two hemispheres, the corpus callosum develops as the largest commissure of the brain. It arises from cells in the frontal and parietal areas of the neocortex. By its growth and the growth of the parts it connects, the more primitive parts of the cerebrum are submerged.

Thirteen areas have been described in the neocortex of the adult rat, thirty-six in the cat and fifty-two major areas, with accessory areas making a total of more than two hundred, as stated above, in man. These are distinguished, as described in chapter 22, by individual variations in the six cortical layers. The internal granular layer (layer IV) shows the greatest variation, becoming much thickened in certain parts of the cortex and disappearing altogether in other parts. This layer is regarded as the receptive layer of the cortex by many neurologists but specific functions of reception, association and projection cannot be sharply ascribed to individual layers of the cortex. All the layers, as pointed out by Fulton, save I and II, receive specific afferent fibers, so no one layer can be regarded as the exclusive receptor. Likewise all the laminae, except layer I, send fibers, either of projection or association, to other parts of the nervous system, so no one layer is the exclusive effector layer. Layer V in the precentral region contains pyramidal cells which give rise to the corticospinal and extrapyramidal motor tracts, but it also gives rise to association fibers. The general pattern of histological structure of the cortex shows that descending axons from layer I carry impulses to layers V and VI. From these layers they are carried upward again by axons of the Martinotti cells to layers II and III. Association fibers end in layers II, III and VI, where their impulses may modify those set up in local cortical areas.

and 6 of the frontal lobe, but according to Fulton, areas 9, 3, 1 and 2, as well as 8 and 19, are included. Sympathetic and parasympathetic effects may be produced separately, with evidence that they are nervous rather than the result of endocrine involvement. Normally the cortical influences on the visceral motor system are inhibitory. Their effects probably reach the blood vessels, glands, etc., through the hypothalamus and its pathways for visceral motor conduction.

SENSORY CORTEX

Study of the living human cerebral cortex has necessarily been limited to favorable cases associated with surgical exposure. Some of these clinical studies have been made on almost experimental planes of accuracy. In 1909 Cushing reported the results of stimulating parts of the cerebral cortex of a conscious patient being operated for cerebral tumor under conditions that forbade a general anesthetic. With the coöperation of the patient he found that stimuli applied to the superior part of the postcentral gyrus produced sensations of touch, pressure and temperature which appeared to arise in the lower extremity. Sensations from stimulation of the middle part of the gyrus were referred to the trunk. Stimuli applied to the lower part of this gyrus gave rise to sensations referred to the face. These observations have been confirmed by Foerster and others. Such intensive studies of the cerebral cortex and its various areas by both experimental and clinical methods has resulted in a great mass of information on the various regions of the cortex.

As described in chapter 22, the cerebral cortex has been mapped out by Brodmann, Economo and the Vogts into a large number of histologically different zones, more than 200 being recognized in the human cortex by the last named investigators. To a limited extent special receptive or effective functions have been attached to various areas in addition to those already named, but correlation of structure and function is far from established for the brain as a whole.

ARCHICORTEX, PALEOCORTEX AND NEOCORTEX

The studies of Tilney on lower mammals indicate that there are three stages in the development of the cerebral cortex, namely, archicortex, paleocortex and neocortex. The archicortex is the most ancient and includes the indusium griseum, the dentate gyrus, the subicular and presubicular areas, and adjacent parts. Together with the olfactory bulb, the archicortex forms the oldest part of the cortical apparatus for elaboration of sensory stimuli. The paleocortex, including the pyriform and postpyriform areas, the olfactory tubercle, the parolfactory area, the amygdalar and rhinal areas together with adjacent areas, form a zone of transition to the neocortex, both structurally and functionally.

The archicortex and paleocortex are sharply bounded from the neocortex by the rhinal fissure. They are called the allocortex (other cortex) by Vogt be-

cause the parts of the brain included in them do not show the six layers characteristic of the neocortex (isocortex of Vogt). Most of their connections indicate that they are associated with olfactory function. There is some evidence, not conclusive, for adding gustatory and other visceral sensory functions. In mammals which have no olfactory bulb (water mammals like the porpoise) the archicortex is much reduced. Man and primates, with small olfactory bulbs and reduced olfactory sense (microsmatic animals), nevertheless show a very large development of the archicortex. In the opossum, which is one of the most primitive of living mammals, the olfactory centers are greatly developed. The parts of the cerebrum related to smell are the most prominent portions of the cerebral hemispheres, the two sides being connected by the large anterior commissure.

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The sensory projection areas are the gateways for analysis and entrance of impulses into the cortex. The association areas form the mechanism for recombination. The motor projection areas have as their main function the initiation of motor responses, but the entire cortex, through the interrelation of layers as described, functions as a unit in integrating the impulses, past and present, which have impinged on the cortex.

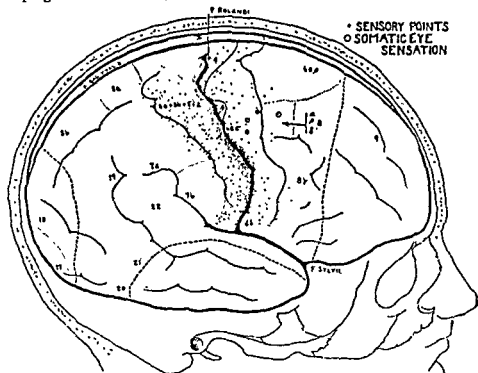


FIG. 231—POINTS IN SENSORY CORTEX AT WHICH STIMULATION BROUGHT FORTH SENSATION IN CONSCIOUS HUMAN PATIENTS.

Black dots represent points producing actual sensory responses referred to some part of the body. After Penfield and Boldrey, from Fulton, *Physiology of the Nervous System*, 1938, Oxford University Press, New York.

PARIETAL LOBE

Electrical stimulation of the upper part of the postcentral convolution in conscious human patients gives rise to sensations of cutaneous stimuli referred to specific parts of the body. When the superior part of the postcentral gyrus is stimulated sensations apparently arising in the lower extremity are felt. The middle portion of the gyrus gives sensations referred to the trunk and upper extremity. In the lower part of the gyrus the sensations are referred to the face. These observations have been confirmed many times. The sensations involved are touch, pressure, sometimes temperature, but never pain. The distribution in the postcentral gyrus (areas 3, 1, 2) of these limb, trunk and face sensory regions is opposite the motor points for the respective parts of the body in the precentral gyrus. It also corresponds to the distribution of the thala-

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macortical projection fibers from the corresponding parts of the body. Stimulation in front of the central fissure produces movement with no sensory phenomena. Stimulation behind the fissure produces either the sensation alone or a sensory experience (aura) related to that produced by stimulation of the specific region involved. This is followed by localized movement of muscles. Areas 5 and 7, according to Foerster, also yield sensory responses on strong stimulation. Application of strychnine to localized areas of the parietal cortex in monkeys (Dusser de Barenne) produces sensations on the body surface so that the animals respond by biting or scratching the skin surface to which the sensation is projected. There is also evidence of disturbance of deep sensibility.

The three major sensory areas of the postcentral gyrus, namely, (1) leg area, (2) arm area and trunk area, and (3) face area, have sharp divisions respected even by strychnine, which generally causes diffuse discharge when introduced into the central nervous system. Sensory impressions may be produced in other parts of the parietal lobe. Many of them are not so sharply localized as those described, and some are entirely unlocalized. The area for sensory projection agrees, as marked out by strychnine, with that shown by distribution of the thalamocortical fibers. The precentral gyrus also is included as a sensory area, according to Dusser de Barenne's results. This does not entirely agree with ablation experiments, but demonstrates that "strychnine, in bringing out the maximum of sensory functions, blurs fine functional differentiation."

Stimulation of a few square millimeters of sensory arm area causes symptoms in both arms, suggesting that the small area of activated cortex serves to "fire off" the whole sensory arm region in the corresponding thalamic nucleus. According to results obtained by Dusser de Barenne, stimulation of any part of the sensory cortex, save the visual, may "fire off" other parts of the cortex. Evidence points to an interaction between the sensory cortical areas and all parts of the thalamus save the medial nucleus. Clinical literature shows that lesions of the parietal lobe may give rise to sensory defects which have a dermatomal distribution. It has been shown experimentally that within areas 3, 1, 2 the surface of the opposite side of the body is represented in a definite pattern which corresponds to the segmental arrangement of the innervation of the body and extremities.

The thalamocortical projection fibers end in areas 4, 6 and in the parietal lobe. Areas 4 and 6 receive the "silent" impulses from the cerebellum from the latero-ventral nucleus. The postcentral gyrus receives the projections relayed from the somatic sensory systems of the spinal cord and the trigeminal nuclei. Correlated studies of the thalamocortical projections and of cyto-architectonic structure of the parietal lobe have shown a number of sensory areas which may have more or less distinct functional significance. However, careful observation and correlation of clinical and experimental data are necessary before this can be established.

It has also been shown that areas 5 and 7 are related to discrimination of

differences in weight. Lesions of the left angular gyrus in right-handed human beings, involving, as a rule, the base of the first and second temporal gyri, produce a type of sensory aphasia, described by Wernicke, in which the patients are unable to understand spoken or written language. They can speak and can write, but their speech is likely to have no meaning and their writing is merely copying. The sigmoid gyrus is necessary to conditioned response to muscle sense stimuli from flexion of a joint. Tactile conditioned reflexes appear to require the coronal and ectosylvian gyri, although the mechanism extends be-

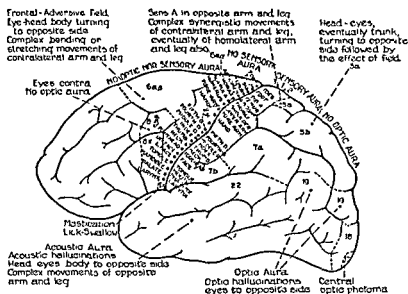


FIG 232—DIAGRAM OF LEFT CEREBRAL HEMISPHERE, SHOWING AREAS WHICH GIVE RISE TO MOVEMENT OR SENSATION WHEN ELECTRICALLY STIMULATED.

Redrawn from Foerster and Penfield, 1930.

yond these gyri. Lashley found that parietal lobe lesions in rats have no effect on learned habits of maze running, manipulation, etc.

In general the parietal lobe contains the projection areas for cutaneous and muscle sense stimuli, together with related association areas.

OCCIPITAL LOBE

Experimental and clinical studies have been consistent in showing visual defects from removal of the occipital lobe in animals and man. One-sided removal results in blindness of the half of both retinas corresponding to the lobe removed. These results were obtained in lower animals by Flourens as early as 1823. They were subsequently confirmed in monkeys and man. Removal of both lobes produces total blindness. In 1911 Minkowski showed in dogs that the visual cortex was confined to the striate area. This has been confirmed in other animals and man, so that area 17 is now recognized as the projection area of conscious vision.

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Lashley showed that in the rat sufficient vision remains in subcortical areas, after extirpation of the occipital lobe, to recognize food, avoid obstacles, etc. The dog can recognize differences of light intensity after the visual cortex is destroyed. It also retains the power to form habits of light discrimination, although total psychic blindness results from the cortical injury. It appears possible that the tectum retains sufficient visual function in the dog for light discrimination. In monkeys light perception is retained, but in man complete and permanent blindness results from destruction of the striate area. All visual reflexes, save the pupillary, are also lost. Blindness in the retinal field of the same side (homonymous hemianopsia) follows radical extirpation of the occipital lobe, but macular vision remains. Removal of the optic radiations with the temporal lobe, however, results in hemianopsia including half of the macula. There appears to have been a phylogenetically progressive assumption of visual function by the higher centers of the nervous system, reaching its culmination in man in assumption by the cortex of almost complete control over visual response.

TEMPORAL LOBE

Auditory Area—It has been known since 1875 that the temporal lobe is concerned with conscious hearing. Ferrier produced deafness in dogs by injury to this lobe. In 1878 Heschl showed that the auditory radiations in man reach the transverse temporal gyri (areas 41 and 42), called after him, which may be regarded as the primary auditory cortex. These gyri receive fibers from the medial geniculate bodies. Area 22 is also related. Stimulation of the auditory areas in conscious human subjects produces ringing sounds (tinnitus) and sensations of buzzing and roaring. Ablation of the temporal lobes does not cause complete deafness but there is loss of acuity, and of recognition of direction of sound and memory for auditory impressions. Bilateral removal of the temporal lobes is followed by disturbances in understanding of spoken language. The transverse gyri of Heschl have been shown by Frazier and Rowe by study of the effect of verified temporal lobe tumors in man to be the correlation and association region of auditory stimuli, i.e., the auditopsychic area. These results have recently been confirmed experimentally in monkeys by Walker.

The symptoms described in man are bilateral, due to connection of each ear to both sides of the cerebral cortex. In some of the patients tested, olfactory disturbances also were found with partial or complete loss of ability to distinguish odors. Uncinate attacks, with responses related to those from olfactory and gustatory stimuli, also are occasionally encountered, as are olfactory hallucinations of disagreeable odors. These conditions are regarded as due to involvement of

to have a vestibular projection area related to the auditory area. Stimulation of the vestibular labyrinth after applying strychnine to the medial part of the temporal gyri produces convulsive movements (Spiegel). Action currents were also increased in

the strychninized gyri. Human patients in which this region is involved in disease processes have sensations of dizziness. No diminution of vestibular reactions or disturbance of equilibrium occurs, however, when the temporal lobe is removed. Anatomically, vestibular fibers have been described to the reticular formation, to the thalamus and to the hypothalamus, but there is little agreement as to their exact course. Spiegel has suggested that the vestibular cortical center lies just medial to the auditory cortex.

FRONTAL LOBE

A number of cases of unilateral removal of the frontal lobe in human patients have been reported. Some defects in thinking and in initiative have been noted, but no general conclusions as to the effect on intelligence can be drawn. Removal of the dominant frontal lobe, as reported by German and Fox, resulted in temporary loss of power of speech (aphonia). This was followed by impairment of the motor, visual, auditory and intellectual components of speech, in various combinations. Removal of the nondominant lobe had no effect on speech, which remained normal.

Amputation of the larger part of both frontal lobes in man, followed by detailed study of the relation between loss of the parts and postoperative psychological effects has been reported by Brickner. There were numerous symptoms, none indicating any alteration in fundamental mental processes, but there was impairment of their completeness. The changes are fundamentally not qualitative but quantitative in nature. Only one function is considered as primarily affected. This is the elaborate association or synthesis into complex structures of the simpler engrammic (latent memory pictures) products associated in the more posterior parts of the brain. There is diminution in the amount of this synthesis, placing a limit on the degree of attainable complexity of thought. Through this deficiency the large variety of secondary and tertiary defects becomes manifest and the outwardly manifest personality appears to be greatly altered. While many of the symptoms have an emotional coloring there is nothing to indicate emotional disturbance in the primary sense. The deduction is that the frontal lobes are not intellectual centers in any sense save a quantitative one and that they play no specialized part in intellectual function. They add to intellectual intricacy by increasing the number of possible associations between engrams which already have been combined to a complex degree in other parts of the nervous system.

CLINICAL INTERPRETATION

SOME ILLUSTRATIVE EFFECTS OF LESIONS OF THE CORTEX

The association areas of the cerebral cortex are greatly expanded in the human brain, accounting for its size as well as its complexity of function. The association tracts have a pattern of functional systems, some of which are

racial and some probably acquired. Interference with the association areas or tracts, as by lesions involving the cerebral cortex, produces a variety of defects of sensory and motor type in which projection areas are not involved. There is neither motor nor sensory paralysis. Such lesions may be caused by cerebral tumors, hemorrhage, occlusion of blood vessels or wounds. The functional defects usually produced are known as aphasias. They result from lesions in the dominant side of the brain. In right handed individuals this is the left cerebral hemisphere.

Aphasia may be defined in the broad sense as "loss or defect in symbolizing relations in any way" (H. Jackson). As commonly used the term connotes a loss in ability to understand or to express language, either spoken or written.

Language or speech is the means of conveying ideas from one person to another. Arbitrary symbols or words, standing for ideas, are the vehicles of expression. An object, as a pen, with its various properties and uses, can be brought to mind by a word, spoken or written. "When we react in the same way to a word as we would react to that which the word stands for, we are said to know the meaning of the words" (Purves-Stewart). The word thus replaces the object.

In the aphasias there is loss of memory for the symbols by which ideas are exchanged. The specific type depends on the association area involved and also on the effect of the lesion on the general intelligence of the patient. In many types of brain injuries there is loss of functional continuity between the various brain areas. They are apparently separated functionally by the injury (hence the term *diaschisis*, a splitting apart) in such a manner as to affect the intelligence generally. The aphasias may be motor or sensory. There is disagreement regarding many aspects of interpretation because of the intricacy of the subject. Only a brief summary of recent views, based chiefly on the description of Purves-Stewart (1937), will be given here as an aid in interpreting some of the functions of the cerebral cortex. Marie and Head differ in some important respects in their interpretations.

Auditory sensory aphasia is the result of lesions in the anterior transverse gyrus of Heschl, in the temporal lobe, and adjacent parts of the first temporal gyrus. The patient can hear ordinary sounds, but cannot understand spoken words. If the lesion is subcortical the pathway to the auditory word area is blocked, bringing about word-deafness. The patient is unable to repeat spoken words, to write from dictation, or to understand what is said to him. He is able, however, to read if the optic radiations are not affected by the lesion, and to understand written words. He can speak spontaneously because he retains his memories of spoken speech.

In lesions involving the cortex of Heschl's gyrus the auditory memory of spoken words is lost and there is impairment of thought and confusion of words in speaking. The patient can read aloud and speak spontaneously, but makes mistakes in both.

Visual aphasia is a result of lesions in the angular gyrus of the parietal lobe. There is loss of ability to understand written or printed characters. *Subcortical visual aphasia* is a pure word-blindness caused by lesions in the pathway to the visual word area. The patient is unable to understand written or printed words, or to read aloud (*alexia*) but he can write spontaneously or from dictation. He is, however, unable to read what he has written. *Cortical word-blindness* involves loss of memory of written or printed words and inability to write words (*agraphia*). The patient is unable to write spontaneously, to copy from printed to written characters, to write from dictation, or to read words.

In *motor aphasia* there is loss of articulate speech without other loss. The patient knows what he wants to say but is unable to voice the words. This type of aphasia is regarded as probably due to a lesion which cuts off the center for speech (Broca's area) in the left inferior frontal gyrus, in right handed individuals, from the voluntary motor cortex. This is a coördinating center for the muscles involved in speech, according to some, while others regard it as a memory zone for spoken words.

In *subcortical* or *pure motor aphasia* the patient is able to understand spoken and written language, but he is unable to repeat words he hears, to read aloud or to express his thoughts in spoken words. His mental processes, however, are normal and he can express his thoughts in writing. The motor activity of spoken words alone is made impossible by injury to fibers below the cortex.

In *cortical motor aphasia* the lesions are limited to the cortex of the speech area in the inferior frontal gyrus and adjacent gray substance. Vocal expression of words is impossible, as in subcortical aphasia, and in addition the patient's thought processes are also impaired.

Apraxia is inability to perform purposeful movements, even though they may be more or less automatic, with the limbs and especially the hand. There is no motor paralysis, incoordination of the limb muscles, sensory disturbance or impairment of intelligence. Apraxia appears to be analogous for the limb muscles to motor aphasia of the speech muscles. It is usually associated with lesions of the left hemisphere. This condition may be either sensory or motor. In *sensory apraxia*, due to lesions in the parietal lobe, the patient may be able to see an object but not to recognize it (*agnosia*). On the other hand, in motor apraxia due to lesions in front of the precentral gyrus, the patient may be able to recognize and name an object, but not to use it. *Agraphia*, or inability to write, is a variation of apraxia.

Total aphasia, involving several or all of the speech centers, is due to large lesions and is accompanied by marked mental deficiency.

THE THALAMUS AND THE CEREBRAL CORTEX

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